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Editor: JOHN M. COULTER

January 1913

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THE

BOTANICAL GAZETTE

JANUARY 1913

THE CLIMAX FOREST OF ISLE ROYALE, LAKE SUPERIOR, AND ITS DEVELOPMENT. I

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WILLIAM S. COOPER

(WITH MAP AND FOURTEEN FIGURES)

Introduction

Eastern North America north of Florida and Mexico is divided into two great phytogeographic regions, the eastern deciduous forest and the northeastern conifer forest. In each of these a number of lines of succession may be traced, all those of a region leading to a certain forest type as the final or climax stage. This final type in its large features is determined by climate, and is much the same throughout the region which it dominates. In the eastern deciduous forest the climax type is made up of *Acer saccharum* Marsh (sugar maple) and *Fagus grandifolia* Ehrh. (beech), with the addition of various other species in some portions of the country. The nature of the climax forest of the northeastern conifer region has not hitherto been determined.

Isle Royale lies just within the limits of the northeastern conifer region, barely within, for one of the farthest outposts of the deciduous forest is located on its southwestern end, where there is a considerable area dominated by the sugar maple, in mixture with more northern trees. Except for the maple and a few of its companion species, the flora of Isle Royale belongs strictly to the northeastern conifer region.

The purpose of the present work was to determine the climax forest of Isle Royale, its composition and character, and to trace the various lines of succession leading to it. It is thus a successional study of a small component portion of the northeastern conifer forest.

At the beginning of the investigation Isle Royale was selected as a field of study because it shows transitional features between the two great forest regions, my original purpose being to devote particular attention to the relations between the conifers and the maple. Circumstances made it impossible to give adequate study to the region dominated by the latter, therefore the work developed into an investigation of the balsam-birch-spruce forest (the northeastern climax) and its attendant successions. For a study of the northeastern conifer forest a more centrally located area might have been preferable; for instance, at some point midway between Lake Superior and James Bay. It will be shown, however, that Isle Royale affords a very fair sample of the forest growth of the northeastern region. It also possesses certain very important advantages which would be lacking in a more centrally located area. Because of its insular position the forest has been less liable to destruction by fire, and the many bays and channels separating various portions of the main island and the outlying islets have served as effective barriers against its spread. Though they have occurred many times during the island's history, it is certain that fires have been far less frequent and destructive here than upon the mainland. The forest may thus be studied in a condition that is as near to being undisturbed as will be found anywhere. Comparative freedom from the destructive agency of man is a second advantage. Again, the island has had a simple physiographic history during the present vegetative cycle, and thus the relation of vegetation to physiography may be the more readily made out. Further, the proximity of the lake shores permits the observation of the earliest stages in the establishment of vegetation upon the rock surfaces, these stages being frequently absent or poorly developed in an inland locality. Finally, the fact that the field of study is an island gives definiteness to the area covered by the investigation.

Headquarters were established at the Park Place Hotel on Rock Harbor (sec. 4, T. 66 N., R. 33 W.), and field investigations were carried on upon the island during the summers of 1909 and 1910. Most of the detailed work was done in the vicinity of Park Place, but the coast was visited from Hawk Island to Blake Point on the northwest, and from Blake Point to the head of Siskowit Bay on the southeast. Excursions into the interior were made from various points along this stretch of shore.

The study was undertaken at the suggestion of Dr. HENRY C. COWLES of the University of Chicago. I wish to express my appreciation of his invaluable assistance and co-operation, freely given at all times during the progress of the investigation. I desire also to extend my thanks to Dr. M. L. FERNALD of the Gray Herbarium of Harvard University, who determined all doubtful spermatophytes and pteridophytes, and to Miss EDITH A. WARNER of Brooklyn, N.Y., who determined the mosses collected upon the island, about 80 in number. The nomenclature of the pteridophytes and spermatophytes is that of the seventh edition of GRAY'S *Manual*.

PREVIOUS BOTANICAL WORK UPON ISLE ROYALE

A limited amount of botanical work of taxonomic and ecological nature has been done upon Isle Royale. In 1848 W. D. WHITNEY, acting as naturalist for a government exploring party, made a brief list of plants found upon the island, which was published in the report of the expedition (**24**) in 1851. In 1890, according to ADAMS (**4**), F. E. WOOD made a collection of plants in the vicinity of Rock Harbor and presented them to the University of Michigan. In 1901 W. A. WHEELER (**58**) published a list of noteworthy species, reporting for the first time the strange occurrence of *Fatsia horrida* (devil's club) upon the island.

In 1904 and 1905 Isle Royale was visited by parties from the Museum of the University of Michigan, both equipped for ecological work among plants and animals. The first, under the leadership of Dr. A. G. RUTHVEN (**3**), spent three weeks upon the island, after a month's work in the Porcupine Mountains of the northern peninsula of Michigan. Their explorations were confined to the

southwestern end of the island. In respect to the vegetation the results of this expedition consist in scattered ecological notes and a list of plants including only 91 species (**49**).

The second party, headed by Dr. C. C. ADAMS, devoted all its time (about six weeks) to Isle Royale, and the resulting report is incorporated in a volume of more than 400 pages (**4**). The botanical work was done by HOLT (**33**), whose report comprises a ten-page account of the plant societies, and an annotated list of lichens, mosses, ferns, and seed plants, including 364 species. There is also much of ecological value to be found in the sections by ADAMS, and the report by GLEASON upon the ecology of the invertebrates (**29**).

Two papers by the present writer (**12**, **12***a*) should also be mentioned, as they were suggested by observations upon Isle Royale.

TOPOGRAPHY AND PHYSIOGRAPHIC HISTORY

Isle Royale is situated in the northwestern part of Lake Superior in lat. 48° N., long. 89° W., about 25 km. distant from Thunder Cape, which is the nearest point of the Canadian mainland. The island is elongated, extending northeast and southwest, and its dimensions are 72 km. by 14 km. at the widest part. It is formed of several parallel ridges which are made by the resistant centers of successive outcrops of a series of Keweenawan lava flows. These dip southeastward at angles varying from 5° to 40°. The southeast slopes of the ridges are gentle, corresponding with the dip of the beds, while the northwest faces are steep and broken, often precipitous. Several of them extend into the lake at either end of the island as promontories or rows of small islands (fig. 1). The largest, the Greenstone Range, stretches the whole length of the island, and is continued northeastward in Passage Island and Gull Rocks. At several points it reaches an altitude of more than 150 m. above the lake level. Between the ridges are narrow valleys, corresponding with the less resistant peripheral portions of the flows and the sedimentary layers that are interbedded with them. These contain many lakes, and where submerged at the ends of the island form narrow fiord-like harbors and channels. The drainage is well adjusted to structure, the streams flowing along the strike

of the less resistant beds, entering the lake at the ends of the valleys, or occasionally through narrow cross valleys, most of which are due to faults.

The quaternary history of Isle Royale is briefly as follows: At the beginning of the glacial period the topography, produced during a long period of subaerial erosion, was essentially as now. The ice completely covered the island, moving southwestward nearly with the strike of the beds, but wrought only slight modifications in the topography. Rock basins were excavated in the

FIG. 1.—Southeast across Scovill Point and the outer islands from the slope of the Greenstone Range: Tobin's Harbor in the foreground; Rock Harbor beyond; Lake Superior in the distance.

valleys and many surfaces were smoothed and striated. *Roches moutonnées* are common. Of the little drift that was left behind most was dropped upon the southwest end, and practically all has been rehandled by the waters of the successive postglacial lakes.

Upon the retreat of the ice, Isle Royale was left entirely submerged beneath the waters of Lake Duluth. The remaining history records a gradual emergence corresponding with the repeated changes of the water level as the lake found successively lower outlets. That this emergence was frequently interrupted is shown by the beaches, sea cliffs, and wave-cut terraces that occur at various altitudes, corresponding with similar ones along the

mainland coast. These indicate periods when the water level was stationary for a considerable time. According to LANE (**36**) the present shore line is more strongly marked than any at higher levels. "Nor is it surprising," LANE remarks, "that the lake level should now be tolerably constant, for Lake Superior now drains over a rock threshold." In comparatively recent post-glacial time (since the formation of the very recent Nipissing beach) tilting occurred in the Lake Superior region, with uplift northward. This must have modified more or less the drainage conditions upon Isle Royale. It is important to bear in mind the self-evident fact that never since its first emergence from the waters of Lake Duluth has Isle Royale been connected with the mainland.

For further geologic and physiographic details the reader is referred to LANE'S report (**36**), to which I am indebted for the material for this brief sketch; and also to ADAMS (**4**), who discusses the physiographic history of the island with considerable fulness. ADAMS also gives much valuable data concerning the influence of the lake storms and surface currents upon the biota of the island.

PHYSIOGRAPHIC AGENCIES NOW AT WORK

The agencies that are now modifying the surface of the island, which are of course the same that have been active throughout its history, may be considered under two heads.

Among the DESTRUCTIVE agencies, *weathering* is of the greatest importance in its influence upon vegetation. It is most evident upon the steep northwest slopes of the higher ridges. Here there are somewhat extensive talus piles lying at the bases of cliffs, or in some cases occupying the whole slope, the cliff having been buried by the accumulation of fragments. In many places the talus is fully clothed with climax forest, in others the fragments are bare or merely lichen covered. The results of weathering are evident also upon the bare rock shores, where scales and plates are seen to have been split from the rock surfaces through the agency of temperature changes. Very important, though effectually concealed, is the chemical action which is going on beneath the humus carpet that covers most of the island's surface. Between the humus and the bed rock there is nearly everywhere a layer of

small rock fragments mixed with organic matter. Most of these fragments are so decomposed that they can be cut easily with a knife. The bed rock itself frequently shows the effect of chemical action. Vegetation is here seen as an important physiographic agent.

Stream erosion is of trifling importance upon Isle Royale because of the small size and low gradient of most of the streams and their freedom from transported materials, necessary as agents of abrasion.

Wave erosion is the most conspicuous of destructive agencies. The surf is actively cutting into the land, and the shore features at the present lake level are very pronounced. At many points along the southeast coast the normally gentle slope of the shore has been transformed into terrace and cliff. In some parts of the abrupt northwest shore the waves are undermining the climax forest itself. In connection with erosion by waves should be mentioned the work of ice, the precise effects of which could not be determined in summer study.

Under the head of CONSTRUCTIVE agencies come deposition by streams, waves, currents, and vegetation. The only notable instances of stream deposition are the few deltas, the materials for which were derived largely from the glacial drift and the products of wave erosion at former levels. The subject is treated further under the head of "Delta swamp succession." The fragments eroded by waves are deposited in the form of beaches and bars, in coves and harbors. Shore currents are effective in transporting the material, and in sweeping the finest into sheltered bays, where it is dropped in the quiet waters. The work of vegetation consists in the formation of peat and humus. Plant life here again appears as a physiographic agent of great importance.

CLIMATE

ADAMS (**4**, pp. 41–44) has described in some detail the climate of the general region, his data being obtained from the records of the Weather Bureau at Port Arthur. The following summary (table I) is derived partly from ADAMS' account and partly from more recent data from Port Arthur obtained through the courtesy of the Canadian Weather Service.

TABLE I

NORMAL TEMPERATURE AT PORT ARTHUR FOR THE 20 YEARS 1888–1907

	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yr.
° C.....	−13.9	−13.7	−7.2	1.7	7.7	13.6	16.8	15.6	11.6	5.3	−2.8	−9.8	2.1

The average maximum temperature for the ten years 1896–1905 was 30.1° C.; the average minimum for the same period was −34.9° C. The mean monthly temperature was below 0° C. for five months, and the mean monthly minimum below 0° C. every month except June, July, and August. The growing season is thus short, including about four months, or even less, between the middle of May and the middle of September. The long northern period of daylight compensates somewhat for the short season.

TABLE II

NORMAL PRECIPITATION AT PORT ARTHUR FOR THE 20 YEARS 1888–1907

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
cm.....	1.77	1.31	2.44	4.18	5.56	7.67	9.82	7.77	8.23	6.49	3.15	1.77	60.16

It is here seen that the greater part of the precipitation takes place during the growing season; 39.05 cm., or more than three-fifths of the total, occurs during the months May–September. The snowfall is rather light; during the six years 1900–1905 the average was 61.03 cm. Reduced to water this amounts to a precipitation of 6.1 cm., which is about one-tenth of the average total for that period.

The evaporation rate is doubtless low because of the low temperature, but there are no data available. This and the relatively abundant precipitation during the growing season seem adequate to account for the extreme mesophytism of the forests of the region.

Since 1906 temperature and precipitation records have been kept during the season of navigation by Captain MALONE at the lighthouse on Menagerie Island. This is one of the Isle Royale archipelago situated 4 km. distant from the nearest point of the main island. During the summer of 1910 I kept thermograph and rain gauge records at Park Place. There is therefore opportunity

for a partial comparison of the insular climate with that of the mainland. Summarization of the records for Port Arthur, Park Place, and Menagerie Island gives the following results:

TABLE III

TEMPERATURES ° C.

		June	July	August
Port Arthur	Mean maximum	23.4	23.9	21.3
	Mean minimum	10.4	11.7	10.0
	Mean daily range	13.0	12.2	11.3
Park Place	Mean maximum	....	21.4	21.4
	Mean minimum	....	12.4	12.9
	Mean daily range	....	9.0	8.5
Menagerie Island	Mean maximum	17.0	18.8	19.4
	Mean minimum	7.1	10.5	13.1
	Mean daily range	9.9	8.3	6.3

From this table we see that the maxima upon Isle Royale are lower than upon the mainland, during the summer at least. Menagerie Island, most under the lake's influence, is the lowest, and Park Place, upon the main island, is intermediate. We may infer that as a result of lower temperatures the evaporation is less upon Isle Royale. ADAMS (**4**, p. 44) suggests that insular location and imperfect drainage probably operate to reduce evaporation. The table also shows that the Isle Royale climate is characterized by less pronounced daily temperature changes than is that of the mainland. The daily range is shown to be uniformly greatest at Port Arthur, intermediate at Park Place, and least at Menagerie Island.

A further comparison (table IV) brings out the fact that the proximity of the lake retards the opening of the growing season, but also that the same factor prolongs it into the fall.

TABLE IV

MEAN MONTHLY TEMPERATURES (° C.) MAY–NOV.; AVERAGE 1906–1909

	May	June	July	August	Sept.	Oct.	Nov.
Port Arthur	7.9	13.6	16.9	15.9	11.6	5.7	−1.7
Menagerie Island	4.3	8.9	11.6	14.4	12.6	6.8	1.9

Evidencing the retardation of the season is the fact that ice frequently remains in sheltered places on the northwest coast of the island into July. I have seen a deserted mine shaft filled solid with ice on July 4. FOSTER and WHITNEY report ice "under the shade of crags, and among the thick evergreen swamps of white cedar."

In precipitation there is apparently not much difference between Port Arthur and Isle Royale, at least during the growing season. As far as the records go the mainland has a slight advantage.

TABLE V

AVERAGE PRECIPITATION MAY–NOV., 1906–1909

Port Arthur	48.00 cm.
Menagerie Island	43.74 cm.

From the foregoing data, which unfortunately are rather fragmentary, it appears that there is at present no ground for concluding that the island climate is effective in producing a more mesophytic type of vegetation than that of the mainland, or vice versa. The lower evaporation rate upon the island, due to lower temperature, is balanced by a less precipitation during the growing season; and the growing season, although retarded in its commencement upon the island, is apparently as long as upon the mainland. The question cannot fully be settled without fuller precipitation records from Isle Royale and a determination of the actual evaporation rates in the two localities. The data presented, however, indicate, so far as they go, that the insular position of the field of study does not seriously affect its value as a fair sample of the region dominated by the northeastern conifer forest.

Part I.—The climax forest

The forest that completely clothes the surface of Isle Royale, with the exception of a part of the bog areas, some limited stretches of xerophytic character, and the small portion dominated by the maple, is made up largely of three trees: *Abies balsamea* (L.) Mill (balsam fir), *Betula alba* L. var. *papyrifera* (Marsh) Spach (paper birch), and *Picea canadensis* (Mill) BSP (white spruce). The studies embodied in the present paper show that this type is the

climax forest of that portion of the northeastern conifer region under consideration; in other words, that upon Isle Royale it is the final and permanent vegetational stage, toward the establishment of which all the other plant societies are successive steps. It is the "climatic" forest of the region, permanent while the climate remains essentially as now.

The evidence in support of this conclusion lies along four lines: (1) extreme mesophytism of the forest; (2) its uniformity of development; (3) all successions lead to it; (4) maintenance of equilibrium. These lines of evidence will now be considered in order.

1. MESOPHYTISM.—The balsam-birch-white spruce forest is the most mesophytic of all the plant societies of the island. The truth of this statement will appear during the discussion of other points and so no further treatment is necessary here.

2. UNIFORMITY OF DEVELOPMENT.—In all places where it occurs, whether upon rock surfaces or reclaimed bogs, upon the part most recently emerged from the lake or upon the highest ridge, the dominant forest is essentially uniform in character. The tree species are the same, and they bear everywhere the same relations to each other.

3. ALL SUCCESSIONS LEAD TO THE BALSAM-BIRCH-WHITE SPRUCE FOREST.—In a later portion of this paper the various successions are treated in detail, and it is shown that all end with the establishment of the balsam-birch-white spruce forest. In other words, those phases of the vegetation that are not uniform in character with the main forest mass are plainly tending toward uniformity. The successions upon Isle Royale may be classified as follows:

A. Primary successions
  I. Xerarch[1] successions
    1. The rock shore succession
    2. The beach succession

[1] The terms *xerarch* and *hydrarch* are here used for the first time, for the purpose of indicating a natural and important classification of plant successions. The former is applied to those successions which, having their origin in xerophytic habitats, such as rock shores, beaches, and cliffs, become more and more mesophytic in their successive stages; the latter to those which, originating in hydrophytic habitats such as lakes and ponds, also progress toward mesophytism.

II. Hydrarch successions
   1. The bog succession
   2. The delta swamp succession
B. Secondary succession
   The burn succession

4. MAINTENANCE OF EQUILIBRIUM.—It has been possible to state with brevity the three points that have so far been presented; indeed, to one visiting the island they are almost self-evident. The validity of the fourth is not so plainly to be seen.

Both observational and experimental studies have shown that the balsam-birch-white spruce forest, in spite of appearances to the contrary, is, taken as a whole, in equilibrium; that no changes of a successional nature are taking place within it. Superficial observation would be likely to lead to exactly the opposite conclusion. In the presence of the other good evidences of permanence outlined in the preceding paragraphs, it became necessary to seek for an explanation of the seeming condition of rapid change that was apparently so plain in the forest. The solution was found in the course of a detailed study which included (1) the characteristics and life history of each tree species and of certain of the lower forms which were of importance, and (2) all the processes and changes brought about through the interrelations of the forest species, discovered by intensive study of a number of limited areas of definite size (quadrats), with every available source of evidence laid under contribution; in other words, an attempt at a thorough investigation of the dynamics of the forest. In the following discussion the results will be given under three heads: I. Description of the forest; II. Studies of individual species; III. Quadrat studies.

I. DESCRIPTION OF THE FOREST

For the sake of concreteness I have selected a definite locality for description, bearing in mind, however, that such a thing as a piece of forest of limited extent which is "typical" of the growth of a region hardly exists.

Smithwick Island (sec. 4, T. 66 N., R. 33 W.) was the selection for this description and for particular study, because the outer row of small islands inclosing Rock Harbor had the appearance of

having been least disturbed by accidental conditions such as fires; and of these islands Smithwick was the most conveniently situated. So primeval and luxuriant is the aspect of the forest here that at first it seemed almost safe to assume that the island had never been burned over since its emergence from the lake. I found, however, in one place, at a depth of one-third of a meter, a layer of carbonaceous material with fragments of charcoal. It is certain then that fire, to an unknown extent, has entered into the history of the island, notwithstanding the many indications to the contrary. Nevertheless, granting that the island may have been burned over at some time, it is plain that the forest has long since returned to its natural condition and may fairly be taken as a suitable area for the study of the climax state. We may be sure that the forest on Smithwick Island has not been disturbed for many hundreds of years at least, and this is not often the case on the main Isle Royale.

There is one somewhat abnormal feature of the conditions surrounding these outer islands that should be mentioned, namely, that the exposure to the strong lake winds is greater than on the main island, and that the death-rate among the trees is thereby increased, and not always proportionally among the different species. On the whole, though, this added exposure merely intensifies certain processes that are in operation everywhere, and thus renders them easier of observation.

The average elevation of Smithwick Island is about 7 m. The southwest one-third was thoroughly burned over about 15 years ago. The forest covers the unburned portion almost completely, being bordered along most of the Rock Harbor side by a narrow shingle beach, and on the lakeward edge by a belt of bare sloping rocks, frequently interrupted by broken or precipitous sea cliffs.

Seen from Rock Harbor the forest has the following appearance, and this description will apply fairly well to the climax forest of Isle Royale in general (fig. 2). The first impression is of great density, the thick foliage extending to the ground at the edge of the forest, allowing no view into the interior. The sky line is ragged, made up of an irregular combination of sharp points and rounded curves, due to the mixture of broad-leaved trees and conifers.

Above the general level of the treetops tower occasional very old white spruces, conspicuous features in spite of or rather on account of their fewness. The paper birches make considerable show by reason of their thick tops, often appearing to compose at least half of the forest, but in reality not much more abundant than the spruces. The balsams are plainly very abundant, and are actually even more so than they seem, since many small ones are hidden by other trees. There are a few large specimens approaching the spruces in size, and thick groves of medium-sized trees are just

FIG. 2.—Exterior view of the climax forest upon one of the row of islands bounding Rock Harbor on the southeast: two tall white spruces at the right; a group of balsams at the left; several large birches.

visible, their spirelike tips appearing in dense clusters among the birch tops. The forest toward the harbor is bordered by a belt where *Alnus crispa* (Ait.) Pursh (green alder) is common, filling in the gaps between the trees. In this region *Pyrus americana* (Marsh) DC (mountain ash) is also frequent, and *Thuja occidentalis* L. (arbor vitae) is occasional.

Upon entering the forest we seem in many places to be in the midst of a dense growth of nearly pure balsam. The individuals of this species are of all sizes, and there is a pronounced tendency among them to grow in close groups. The small trees (roughly

those 7 m. high and under) are greatly in excess of the larger ones. There are also numerous dead and dying specimens, almost always small ones, some of the dead trees showing evidence of having succumbed very recently, the needles not yet having dropped off. The occasional large trunks of the birches are conspicuous objects, but young ones are not numerous. It is often difficult to find a single spruce, unless one has carefully estimated from the exterior the position of one of the conspicuous old specimens. Young spruces are exceedingly rare, so that a long search will be necessary to discover one. The shade in most parts, especially under the closely placed balsams, is dense, though there are frequent partial openings, caused principally by windfalls (fig. 3). Standing dead trees of large size are very rare, but fallen trunks in all stages of decomposition are numerous, the greater number being balsams, though the dead birches are more conspicuous on account of their greater size.

FIG. 3.—Illustrates conditions resulting from a windfall in the climax forest: fallen trunks and young balsams; Smithwick Island.

Shrubby growth is not abundant. The areas of not too dense shade are often thickly populated with *Taxus canadensis* Marsh (ground hemlock). Other large shrubs that are more or less frequent are *Alnus crispa* (Ait.) Pursh (green alder), *Viburnum pauciflorum* Raf. (high bush cranberry), *Sambucus racemosa* L. (red-berried elder), *Lonicera canadensis* Marsh (bush honeysuckle), *Fatsia horrida* (Sm.) B. & H. (devil's club), the last abundant in one restricted area.

The herbaceous growth is sparse except in partial openings.

Most prominent is the association of about eight herbs which is so characteristic of the northeastern conifer forest, and in part of similar forests over a much wider range. The group includes the following: *Cornus canadensis* L. (bunch-berry), *Trientalis americana* (Pers.) Pursh (star-flower), *Linnaea borealis* L. var. *americana* (Forbes) Rehder (twin-flower), *Maianthemum canadense* Desf. (two-leaved Solomon's seal), *Clintonia borealis* (Ait.) Raf., *Mitella nuda* L. (mitrewort), *Aralia nudicaulis* L. (wild sarsaparilla), *Coptis trifolia* (L.) Salisb. (goldthread). These species are found in every part of the Isle Royale climax forest, and many of them in the bog forest, bogs, and along the rock shores as well. Others, less characteristic and abundant, still occur commonly: *Lycopodium annotinum* L. (stiff club moss), *L. obscurum* L. (ground pine), *Phegopteris Dryopteris* (L.) Fée (oak fern), *Aspidium spinulosum* (O. F. Müller) Sw. (shield fern), *Polypodium vulgare* L. (polypod), *Cystopteris fragilis* (L.) Bernh. (fragile fern), *Moneses uniflora* (L.) Gray (one-flowered Pyrola), *Ribes prostratum* L'Her (fetid currant), *Epipactis repens* (L.) Crantz var. *ophioides* (Fernald) A. A. Eaton (rattlesnake plantain), *Oxalis Acetosella* L. (wood sorrel), *Habenaria obtusata* (Pursh) Richards, *Comandra livida* Richards.

By far the most important part of the herbaceous vegetation, both quantitatively and ecologically, is the moss contingent. This forms a nearly continuous carpet, being absent only where the shade is very dense. Three species are chiefly concerned, and these are quite equally distributed, one usually being dominant in a given spot. *Calliergon Schreberi* (Willd.) Grout (*Hypnum Schreberi* Willd.) is perhaps the most abundant, and grows in the drier places alone, as well as mixed with the other two in general. *Hylocomium proliferum* (L.) Lindb. usually covers the areas of well decomposed humus; while *Hypnum crista-castrensis* L. seems to prefer rotten wood. Next to these in abundance is *Hylocomium triquetrum* (L.) Lindb.

The humus soil, which is composed largely of moss remains, tree waste, and rotten wood, varies in depth from 0.25 to 6 dm., the average being perhaps about 3 dm. It rests directly upon the smooth rock surface or is separated from it by a loose layer of decomposed fragments.

Returning to the trees, the first conclusion would naturally be that we have here a stage in the succession approaching but not having reached the final or climax condition. The spruces and birches appear like relicts, and the balsams, which seem to be of all ages, but mostly younger than the trees of other species, are apparently succeeding them. The seeming probability is that before long the birches and spruces will have died out, leaving a pure growth of balsam which in the future will succeed itself. Appearances of this kind have sometimes been considered sufficient to prove that succession is in active progress, and there are undoubtedly many cases where the phenomena are not deceptive. In no case, however, should the mere appearance of rapid succession be admitted as valid evidence until verified by surer methods of study. The results of an attempt to use such methods are detailed in the two following sections.

II. STUDIES OF INDIVIDUAL SPECIES

ABIES BALSAMEA (balsam fir).—If it be objected that the forest is after all a practically pure stand of balsam, with a mere scattering of other species, the following facts will be sufficient answer. It is true that in number of individuals, all sizes considered, the balsam is greatly preponderant. Of the 254 trees included in the six quadrats soon to be described, 78.7 per cent are balsam. But if we take account only of those trees which may be considered as forming the mature stand, the percentage of balsam becomes much smaller. Size, not age, is here the proper criterion. Considering those trees which are 1.25 dm. and more in diameter, which is a rather low limit to set, the proportion is only 56.7 per cent. Among the larger trees the balsams are still less numerous, making only 33.3 per cent of those 2.5 dm. and more in diameter (fig. 4). The same facts are shown when age is considered instead of size, though in a somewhat less striking manner (fig. 5).

Two causes are responsible for the preponderance of balsam in the young growth. First, the seedlings make a successful start in almost any sort of situation, provided sufficient light be available. Very young seedlings were seen commonly in such diverse situations as the following: natural openings in the forest caused by

windfall, in moss and humus (by far the commonest situation); windfall opening in cedar swamp, in moss; rotten logs in forest

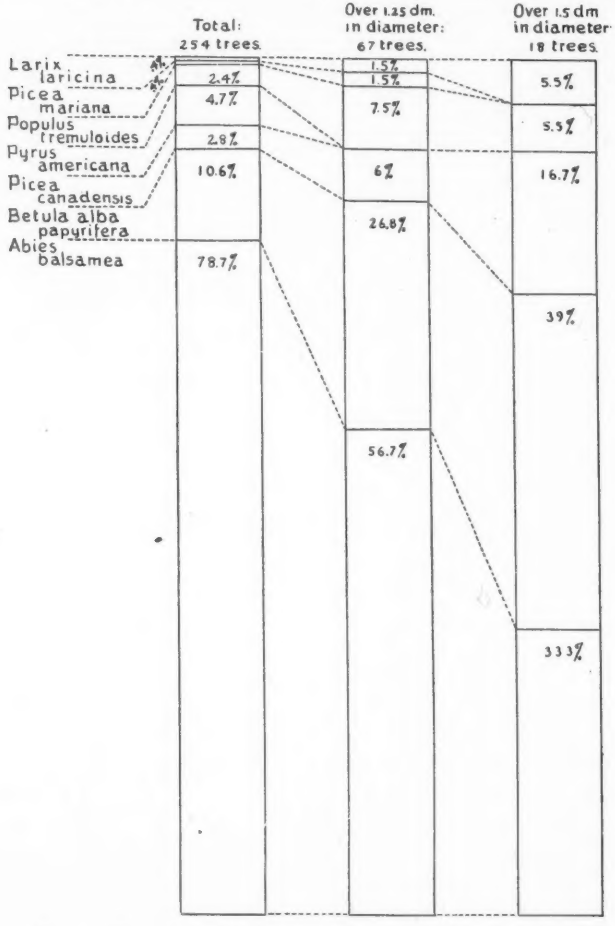


FIG. 4.—Composition of the climax forest; according to size of trees

(infrequent in this region); open bogs in sphagnum; crevices and humus-filled depressions on rock shores; burned areas, both forested and bare, not abundant; upper beach among large shingle,

in partial shade and entirely open, abundant in one locality; sand bar across mouth of small stream, abundant. The entire absence

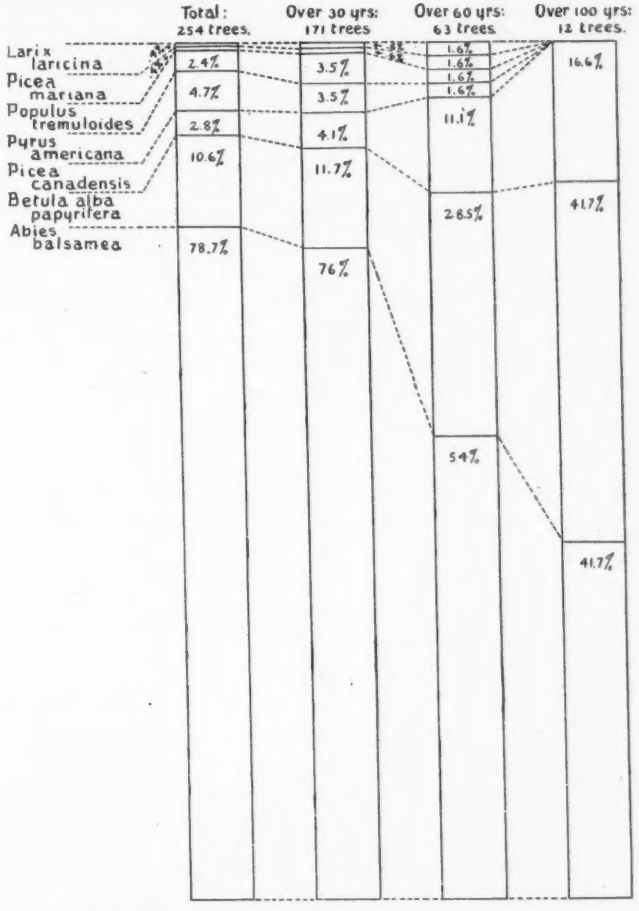


FIG. 5.—Composition of the climax forest; according to age of trees

of very young seedlings wherever the shade is even moderately dense is noteworthy. Later in life the young trees can endure severe shading, but for a successful start abundant light seems to

be a necessity. The possibility must be admitted that light (or rather radiant energy) is only indirectly the important factor, its influence lying in its effect upon the seed bed. Densely shaded soils upon Isle Royale are nearly everywhere more or less of the nature of peat, low in temperature, soggy with unavailable water, and probably like peat deficient in certain types of bacterial and fungal life. The obvious effects of abundant access of radiant energy would be to partially cure the sogginess of the soil and thus increase its oxygen content, and to bring about a high soil temperature; both of which changes would result in greatly increased activity among the various types of soil organisms. Plans to carry out some experiments with a view toward determining the germination conditions of the balsam and other trees were frustrated by the total failure of the seed crop in 1910.

A second cause, which easily accounts for a considerable part of the young growth of balsam, is found in the habit of layering, by which that species reproduces abundantly. All the other conifers of Isle Royale except the pines possess the habit too, but to a much less degree. In a previous paper (**12**) I have described in detail the layering habit of the balsam and other conifers, and therefore a few words here will be sufficient. In the forest one frequently comes upon small groups of young balsams, composed often of about half a dozen individuals of various sizes. Upon superficial inspection these would easily pass for a cluster of seedlings, but if the group be carefully dug up it will be found that the young trees are all connected with each other just below the surface of the ground. The group comes into existence in the following manner. One or more of the earliest branches of a young tree (which is sometimes hardly beyond the seedling stage) comes to be slightly covered with humus and litter, and produces roots. The tips then become erect, and taking on radial symmetry are transformed into miniature trees. By successive layering of branches as many as five generations produced in this manner may be included in a single group. Large drooping branches of mature individuals may layer in the same way, and it is not uncommon to find an old trunk surrounded by a circle of daughter trees developed from layered branches. The young shoots soon come to depend entirely

upon their own root systems for sustenance, and there is evidence that a considerable number of them become independent through the decay of the connecting branch. The habit is so common in the Isle Royale forests that a large proportion of the apparent balsam seedlings may be accounted for in this way.

The preponderance of balsam in the young tree growth being accounted for, it is now necessary to explain its rapid decrease when greater size and age are considered. Several causes combine to bring this about. Abundant germination is itself a disadvantage, since it results in severe competition, much of the stand undergoing suppression and finally death. The species is very susceptible to fungus attacks and to diseases of many kinds. Rotten-hearted trees are very common. Witches' brooms caused by a rust (*Peridermium*) are familiar objects. According to MOORE and ROGERS (41), the liability to fungus attack is greater in pure stands than where trees are scattered. The common group habit of the species is therefore a disadvantage in this respect. The prevalence of heart rot, together with the natural brittleness of the wood, cause extreme liability to windfall, and broken trunks are a common sight, while uprooted balsams are rare. It is not surprising, in view of these facts, that in spite of its prolific power of germination the balsam never reaches the position of dominance in the mature stand. In a word, its high birth-rate is balanced by a high rate of mortality.

BETULA ALBA var. PAPYRIFERA (paper birch).—The prominence of this species in the mature stand and in the general aspect of the forest has been noted, and also its comparative scarcity in the young growth. It is certain that the germination of the birch in this region is far from prolific. Very young seedlings were frequently seen, and in situations almost as varied as those inhabited by the balsam, but never in abundance as in the case of that tree. I quite frequently found very small seedlings in dense shade, but they were never more than five or six years old, indicating that conditions (probably light supply for photosynthesis) were not favorable for continued growth. Opportunity for successful reproduction comes usually, as in the case of the balsam, after windfalls (fig. 8). On account of its much less prolific germination the birch is far less

abundant in such situations than the balsam. Its growth under the same conditions seems to be somewhat faster, however, and so the few birches of the windfall area, or some of them, soon overtop the balsams and cause the suppression of many of the latter, at the same time, with the aid of the balsams, temporarily preventing further reproduction of either species. Paper birch has comparatively few and ineffective fungus enemies (DANA **18**) and is not particularly susceptible to damage by wind, on account of its elastic branches and extensive though shallow root system. Even when it is broken off in severe storms, as occasionally happens, it has a means of recovery in its ability to send up vigorous sprouts from the stump. Occasional clumps of immense birch sprouts scattered through the forest are evidence of this power. The most effective obstacle to its increase is competition with the balsam in its early stages, and here its greater rate of growth gives it a slight but important advantage. On the whole it may be said with certainty that its low birth-rate is compensated by a very low mortality, and it is thus able to maintain itself in making a good proportion of the mature stand (figs. 4, 5).

PICEA CANADENSIS (white spruce).—This species is ecologically much less important than the first two, occurring only sparingly in most places; but it attains a greater size than the other trees, and is one of the most conspicuous features of the forest. On account of its scarcity little could be discovered concerning its life-history upon Isle Royale. From the few seedlings that were observed it seems probable that abundant light is necessary for its successful reproduction. According to the United States Forest Service (**22**) it is not a prolific seed bearer, and has definite seed years, which in New England are about eight years apart. All the young trees seen were growing in situations where at least fairly abundant light was available. It seems probable therefore that the white spruce is also largely dependent upon windfalls for its successful reproduction in the virgin forest. It is able to withstand severe winds without breaking, as is shown by individuals towering conspicuously above the general forest level. It is not particularly liable to fungus injury. Birth-rate and mortality are both low, and the species is able to maintain its small proportion in the forest.

OTHER TREES.—*Pyrus americana* (Marsh) DC (mountain ash), though fairly common, is of little importance ecologically, since it is very short-lived, never reaches any great size, and produces little shade. Its life history in most respects is similar to that of the birch, and it has the same habit of producing sprouts from the stump. *Pinus Strobus* L. (white pine) is scattered thinly through many parts of the forest, generally towering high above the other trees. Its ecological status seems to be similar to that of the white spruce. There is no indication that in recent times at least it has ever been abundant upon Isle Royale. *Picea mariana* (Mill) BSP, *Larix laricina* (DuRoi) Koch, and *Populus tremuloides* Michx., which are found here and there in the climax forest, will be sufficiently treated in connection with quadrats 5 and 6. *Populus balsamifera* L. also occurs sparingly.

TAXUS CANADENSIS.—The most important of the lower plants of the forest—more important indeed than many of the trees—is the ground hemlock. Its influence lies in the completeness with which it occupies and shades the ground, preventing tree reproduction over large areas. This effect will be noted in connection with quadrats 5 and 6, and quadrat 1 includes part of a ground hemlock area in which trees are practically absent. *Taxus* can endure considerable shading, but is never found in the dense shade cast by the balsam groups. Balsam in its turn is excluded from large areas by *Taxus*, so that the competition between these two species is exceedingly keen. *Taxus* spreads abundantly by underground stems, and in this way invades new areas of forest when conditions are favorable, at the same time dying out in the older portions of the growth, thus allowing other plants to start in such places.

III. QUADRAT STUDIES

The method of investigation whereby a knowledge of the dynamics of the forest was gained was as follows. A rectangular area was laid off, made up of one or more units of 5 m. square, the usual size being a quadrat of 10 m. square, or four units. In the diagram of this area the position and kind of every tree, down to the smallest seedling, was plotted and its diameter noted. Cuts were next made with an ax to the centers of the large trees, and the small

ones were felled. The age of every tree was then determined by counting the annual rings, and note was made in each case of the degree of soundness of wood, width of rings, and periods of suppression indicated thereby. The cuttings were made at the height of about 0.3 m. An element of error is introduced here, making the age as determined a few years too low. It seemed inadvisable, considering the many quadrats to be studied, to use up much valuable time in making the counts absolutely accurate. This would have involved the cutting of every tree at the surface of the ground, a very difficult and slow process. A saw might have been used instead of an ax, but when the rings are at all obscure it is impossible to count them from a sawed surface. I believe that the error introduced does not affect the validity of the results, since it is approximately the same in nearly every instance. The method on the whole gave excellent results, in the study of the rock shores and bogs as well as of the climax forest. Its use was made easy by the comparatively small size of the Isle Royale trees. Sixteen quadrats were studied in all, comprising 74 units of area, and involving the determination of the ages of about 900 trees. If objection be raised that the method is unduly destructive, it may be answered that the cutting over of these small areas produces exactly the same effect as does windfall, a process that is continually taking place, and thus makes possible a new crop.

In addition to the statistical study of the trees, careful notes were taken of the lower vegetation and the physical factors of the habitat. Less detailed studies of many other localities were also made for comparison with the quadrats.

The results of the quadrat studies so far as they concern the climax forest will now be given in detail. The first four described were located on Smithwick Island; quadrats 5 and 6 were upon the main Isle Royale.

Quadrats on Smithwick Island

QUADRAT 1 (fig. 6).—This quadrat exhibits most clearly the relations which the different tree species hold to each other and to the physical conditions of the habitat. It includes but one spruce, an aged giant 250 years old, long past maturity, with sparse foliage,

giving practically no shade. Two healthy birches (105 and 107 years old), close together, produce considerable shade in their vicinity. There are several rather old balsams (64–90 years) well

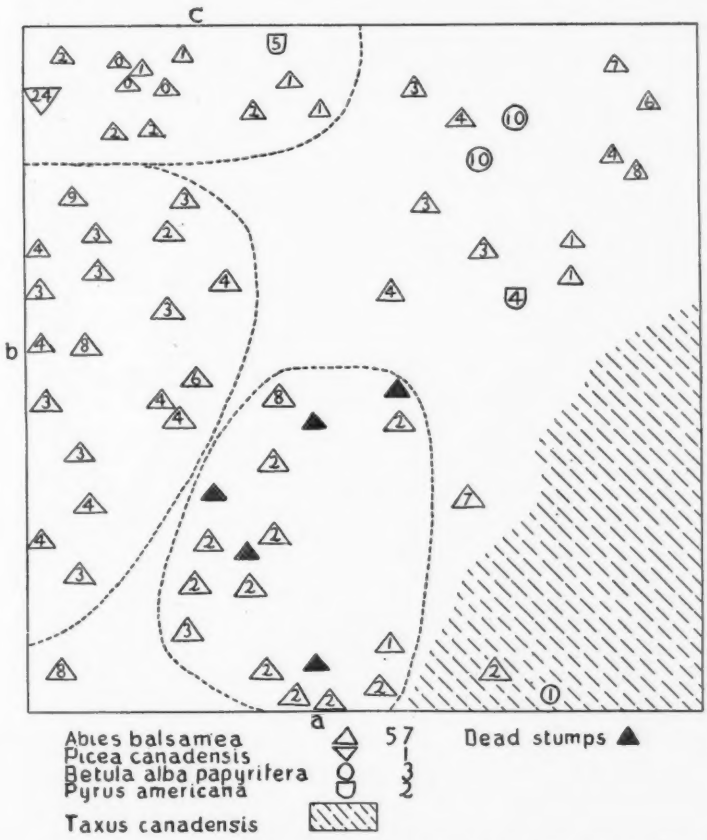


FIG. 6.—Quadrat 1, Smithwick Island: the symbols indicate the species; the numbers within them the ages of the trees by tens; for example, a tree marked *6* is between 61 and 70 years of age.

scattered over the quadrat, and usually more or less isolated from the smaller growth. The young trees are practically all balsams, the only representatives of other species being two mountain ash

(one a clump of three stump sprouts) and a 20-year old birch in the lower right-hand corner. The young growth is not evenly distributed, but shows a tendency toward grouping, which tendency will be seen in each of the succeeding quadrats. The larger number of trees of each group are approximately even-aged. For example, the rather scattered group *a* that surrounds the 5 balsam stumps contains 13 balsams, 10 of which are 23–28 years old. Of the 18 trees in group *b*, 14 are between the ages of 30 and 50, not so uniform as the last, but decidedly of a single generation. Of the 13 trees in group *c*, all but the mountain ash and the large spruce are under 30 years.

Group *a* illustrates in a striking manner the way in which these even-aged clusters come into existence. Within its limits were 5 large rotten balsam stumps from which the trees had been broken a meter or more above the ground. The group evidently constitutes a windfall, probably caused by a single storm, one tree in its fall carrying others with it. Such windfalls of various ages are exceedingly numerous throughout the forest, the balsams, on account of their brittleness and susceptibility to fungus attack, being the ones most frequently destroyed. This particular windfall is of special interest because it was possible to determine the time at which it occurred. One of the large balsams in falling pinned to the ground a young tree of the same species, which, in spite of unnatural position and dense shade caused by the branches of the fallen one, has continued to live up to the present. The younger tree was 49 years old, and the first 12 rings were exceptionally wide, showing that up to the age of 12 years it was an unusually vigorous sapling. At this point a sudden change becomes evident, for the remaining rings are so close that in counting them a magnifying glass was an absolute necessity. This change could have been brought about only by some sudden and violent cause, and this cause is evidently to be found in the fall of the older tree. The windfall is therefore to be dated about 37 years ago. Returning to the trees composing group *a*, we find that they are all balsams; one is 85 years old, another 38, a third 14, and 10 range from 23 to 28; 11 then are subsequent to the windfall, and 10 began life

within a period of six years, 9–14 years after the windfall occurred. There is only one that clearly antedates it.

Upon inquiring as to the cause of these facts, the factor of radiant energy immediately suggests itself (see p. 20). The older balsams, now fallen, when living were close enough to cast a dense shade over the area which they controlled, and there can have been no young trees beneath them, since if there had been, the present generation would antedate the windfall. It was not until 10 years after that event that young balsams began to appear in the area. Radiant energy being the principal factor involved, this interval of a number of years is entirely to be expected, since some time would elapse before the disintegration of the tangle of branches with their persistent needles would allow a large amount of the energy to reach the ground. Evidence in support of this hypothesis was found in every quadrat and in every considerable part of the forest. In no other case was it possible to determine the exact age of the windfall, but the general relation between the older and younger generation was usually plainly to be seen. Frequently the only sign of windfall is in the rotting moss-covered logs, but the close group of even-aged trees, sometimes 50 years old or more, tells the story plainly.

In quadrat 1 two other windfall areas are shown, one (*c*) quite recent, the other (*b*) older. The greater range of age among the trees in these areas suggests that those of the former generation did not all fall together. This type of windfall is commoner than that represented by group *a*. The fall of the first trees gives the wind a better chance to reach others. This slow process may be extended over a long period, even until the new generation has begun to fill in the gaps first made. In contrast to the dense grouping just described is the remaining area of the quadrat, where the individuals are less closely placed and are on the average much older. The part not included in the three groups comprises two-thirds of the area of the quadrat, yet it contains only 18 trees, 7 of which are over 60 years; while the other third of the quadrat contains 45, only 5 of them being over 60 years. The fewer trees in the larger part nevertheless produce a dense shade, and there is very little young growth beneath them.

There is a difference that should be noted between the shade-producing capacity of the balsam and that of the birch. The former, with its many whorls of short branches close together and its opaque leaves, casts an exceedingly dense shadow which does not influence a large area. A moderately close stand of large balsams allows extremely little light to reach the ground. The birch (in its primeval forest form) influences a large area, but its shade is not dense, because of its comparatively thin crown and translucent leaves. Under the shade of large birches there is frequently a scattering of young growth, while under thrifty balsams there is rarely to be found any at all. Both conditions are well shown in the diagram of quadrat 1.

The effect of shading is seen also in the undergrowth. In the dense shadow of the balsams there is a mere sprinkling of herbs, and mosses are usually absent entirely, the ground being covered with a layer of tree waste. It is in shade of moderate density and in openings that the greatest luxuriance of mosses and herbs is found. The ground hemlock is excluded from most of the quadrat for the same reason, but in the lower right-hand corner there is an area completely occupied by a dense growth of it, which effectually prevents the establishment of any other species.

QUADRAT 2 (fig. 7).—This quadrat shows the same features as the last. Group *a* contains a great number of young trees of similar age, mostly balsams, which have started as a consequence of one or more windfalls. Of the 40 balsams in the area, 33 are between the ages of 20 and 35 years, and within these limits, as shown by the diagram, there is a tendency for those of similar age to be neighbors. Numerous fallen trunks represent the former generation. The large balsam marked "12," which was 121 years old—an unusual age for this species—was past maturity, and like the big spruce in the preceding quadrat was ineffective in producing shade. At *b* there is a part of an older group, 5 of the 7 balsams being between 44 and 53 years old. The upper left-hand corner is dominated by a few old and large trees, balsams and birches, with practically no young ones—only a few beneath the birches. The shade in this area was dense and the undergrowth sparse, even the ground

hemlock being nearly absent. No spruce grew in this quadrat, but there were occasional large ones near.

QUADRAT 3 (fig. 8).—This small quadrat of one unit area shows a group of even-aged trees, among which are several young birch

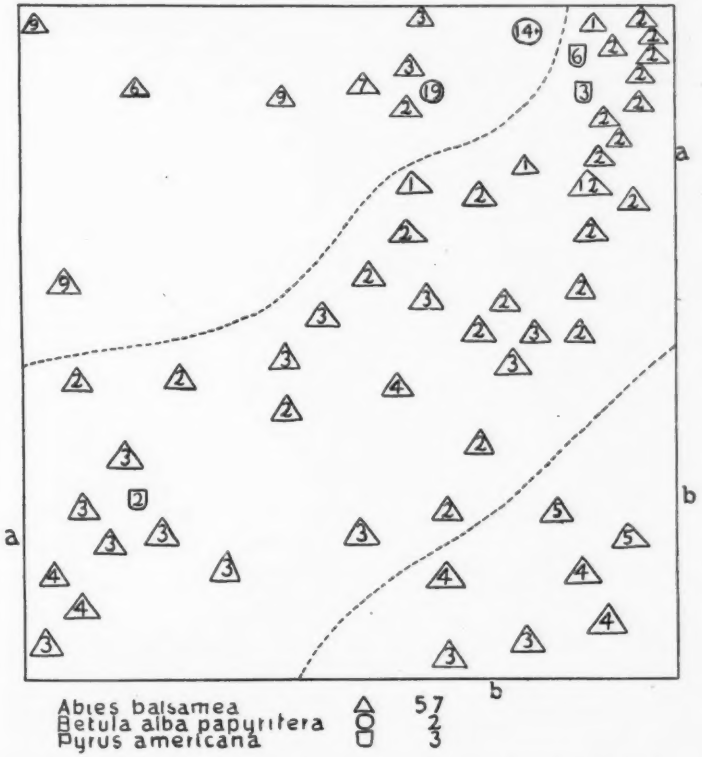


FIG. 7.—Quadrat 2, Smithwick Island; for explanation of symbols see fig. 6

and mountain ash as well as balsam. No living trees of a former generation are present within the limits of the quadrat, but several were seen near. Decayed trunks were frequent and were mostly birch. Of the 37 trees, 26 were within the ages of 26 and 35 years, and the others were very close to these limits. Evidently then all

three species started growth at practically the same time, and the immediate cause was a windfall. The birches are tall and spindling, but now slightly overtop the balsams in spite of a somewhat later start. Having gained the advantage as to light supply, their tops will spread fast, and these trees, or more likely one or two of them, will doubtless finally develop the thick-stemmed, spreading, round-topped form characteristic of mature specimens in the virgin forest. The balsams which are within the sphere of influence of the birches will be suppressed. This process in fact has already begun. The last 5–10 rings of those balsams which were close to the birches were found to be noticeably narrower than the earlier ones, while the rings of those growing isolated from other trees were uniformly spaced. Undergrowth was practically lacking, the shade being everywhere very dense. Even the ground hemlock was entirely absent.

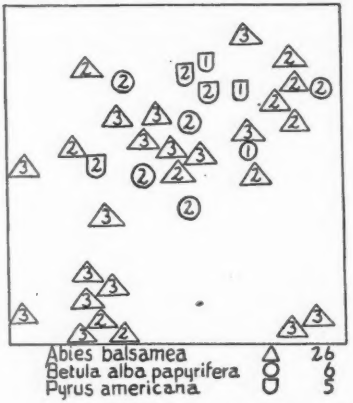
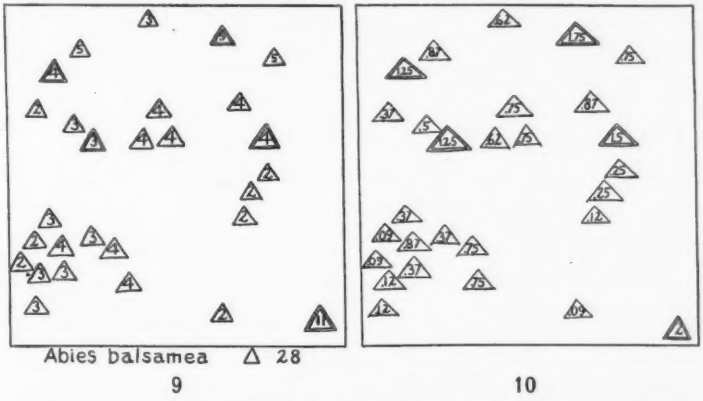


FIG. 8.—Quadrat 3, Smithwick Island; for explanation of symbols see fig. 6.

In this quadrat the mountain ash showed an interesting habit of growth. Several saplings were seen among the closest groups of balsams which were so slender and weak as to closely resemble lianes. One specimen was 4.3 m. high and 2.25 cm. thick at the base, unbranched, with a single tuft of leaves at the top. It was supported entirely by the balsams against which it leaned, and its upper portion had penetrated among the interlacing balsam branches close to the trunk of a near-by tree. It was 16 years old, and had evidently started before the balsams had begun to shade the ground thoroughly, but was left behind in the severe competition for the available light supply.

QUADRAT 4 (figs. 9, 10).—This quadrat, also of one unit area, includes two generations of balsam and no other species. Several large birches were near by and a large spruce. The older generation

is represented by one individual in the lower right-hand corner, well isolated from other trees, 115 years old. The younger generation illustrates competition between individuals of a single species which began life at about the same time. Fig. 9 shows the age of each tree, and fig. 10 its diameter, which, it may be noted, maintains a pretty constant proportion to height. It will be seen from the latter that 4 trees (marked by double symbols) have attained a much greater size than the others; and if comparison be made with fig. 9 it will be evident that these 4 are not noticeably older than



FIGS. 9, 10.—Fig. 9, quadrat 4, Smithwick Island: age of trees; for explanation of symbols see fig. 6; fig. 10, quadrat 4, size of trees; the numbers indicate the diameters of the trees in decimeters.

their neighbors. The annual rings of these 4 trees were found in every case to be wide and evenly spaced, while those of their less favored companions were either very narrow from the beginning or plainly showed recent suppression. This illustrates an important principle in forest study, namely, that no reliance can be placed upon the size of a tree in fixing its age or in determining its place where two or more generations are concerned. These 4 individuals in some way gained the advantage early in life and caused the suppression of their neighbors. Evidence of the severity of the shading was shown by the presence among the living balsams of 20 dead specimens, averaging a meter in height, and in length of

life from 14 to 38 years. Some had been dead for a long time, while others showed evidence, in needles still clinging, of having been alive until very recently. All had undergone severe suppression. In consequence of the deep shade the undergrowth was extremely sparse, except in the lower left-hand corner where there was a partial opening. Here was a luxuriant growth of mosses, including *Hylocomium proliferum* (dominant), *Hypnum crista-castrensis*, *Calliergon Schreberi*, and *Dicranum undulatum*. The close group of young balsams occupying this locality was largely due to layering. Quadrat 4 then includes in the main a group of balsams of very different sizes, giving an appearance of gradual reproduction, but in reality essentially even-aged, and belonging distinctly to a single generation.

Quadrats on the main Isle Royale

It has been said that the conditions on Smithwick Island include one that is somewhat abnormal for the region as a whole, namely, that the exposure to wind is greater. Two quadrats in sheltered localities on the mainland of Isle Royale were studied for the purpose of comparison. They probably represent the opposite extreme so far as exposure is concerned.

QUADRAT 5 (figs. 11, 12) was located a few hundred meters back from the southeast shore of the Blake Point peninsula in sec. 23, T. 67 N., R. 33 W. The locality is thoroughly sheltered from northwest winds by the main ridge, and from the lake winds by the islands to the southeast. On the diagram several points of difference from the preceding quadrats are readily seen. Most noticeable are the greater average age of all species and the absence of very young growth. Two new trees appear: *Picea mariana* (Mill) BSP (black spruce) and *Larix laricina* (DuRoi) Koch (tamarack), each species being represented by one individual. The whole stand is remarkably even-aged, 22 of the 38 trees being between the ages of 82 and 98 years. There is some tendency toward grouping of trees of similar age, though not so noticeably as on Smithwick Island. The group *a* is a very marked one, however. Of the 9 individuals of 4 species composing it, 7 are between 83 and 92 years, and 5 between 89 and 92. The effect of

shelter from wind is very evident in the greater height of the trees. The protection which this area enjoys does not by any means prevent windfall, but merely lessens its intensity, and allows the trees to reach a greater height before they are overthrown. Several

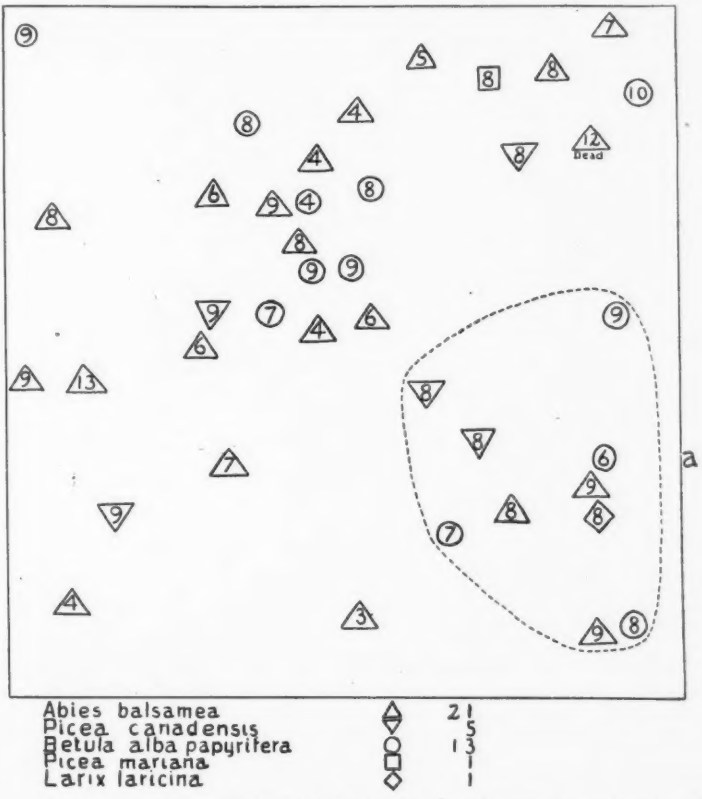


FIG. 11.—Quadrat 5, Blake Point Peninsula: age of trees; for explanation of symbols see fig. 6.

standing dead balsams were seen on this quadrat and they were frequent through the neighboring forest. On the outer islands the balsams almost never die a standing death. Quadrat 5 (fig. 12) also shows suppression of part of the stand, the larger trees being

indicated by double symbols. The absence of very young growth is explained by the fact that the forest floor was covered by a thick mass of ground hemlock.

Black spruce and tamarack are found occasionally throughout the forest. Since they are both very intolerant of shade, they probably make a successful start only where an extensive windfall

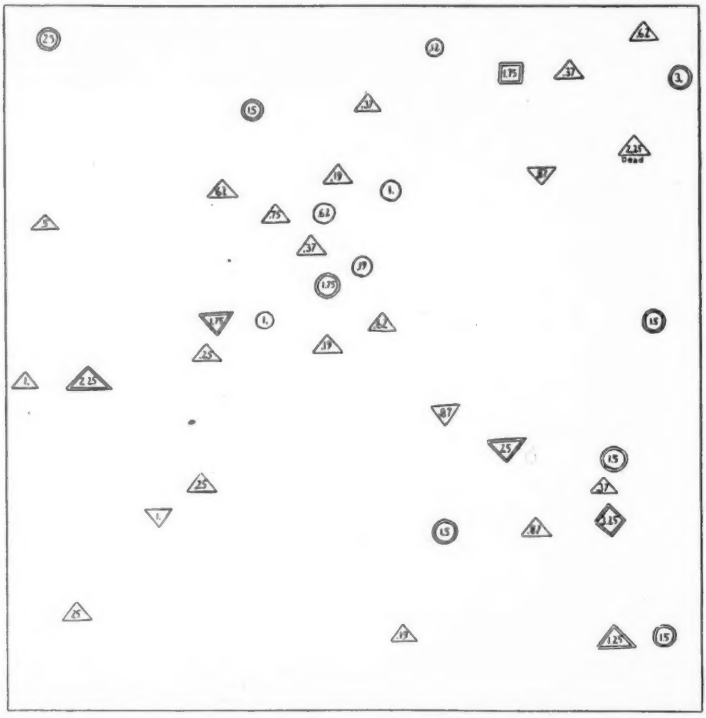


FIG. 12.—Quadrat 5: size of trees; for explanation of symbols see fig. 10

has let in abundant light. The black spruce as a member of the upland forest is abundant in one locality on the southeast shore of Isle Royale and in certain other places. The evidence seems to show that this species in abundance in the upland forest indicates a transitional stage approaching the climax. The subject will be treated again in the consideration of the rock shore succession.

QUADRAT 6 (fig. 13).—The conditions here as to shelter were similar to those of the last. The quadrat was located near the shore of Tobin's Harbor in sec. 33, T. 67 N., R. 33 W. The small number and large size of the trees are noticeable, and also the entire

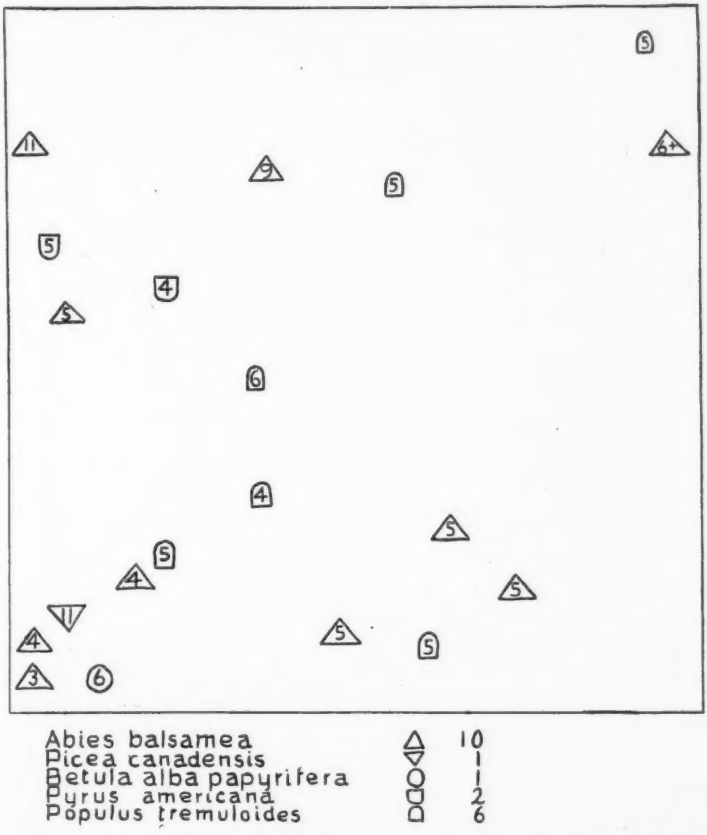


FIG. 13.—Quadrat 6, near Tobin's Harbor; for explanation of symbols see fig. 6

absence of young growth, in spite of the comparative lightness of the shade. These conditions were plainly due to the mat of ground hemlock which practically covered the quadrat. The ground hemlock therefore, rather than any tree species, dominates and

controls this area. The surrounding forest was found to be essentially similar to the sample, except that the cover of ground hemlock was not continuous, and where it was absent the usual conditions of windfall reproduction, especially of balsam, prevailed. The large number of good-sized trees, balsams being specially noticeable, owe their continued existence to the protected position of the area. The presence of *Populus tremuloides* Michx. (aspen) in considerable abundance is noteworthy. This species seems to be ecologically equivalent to the birch, except that it does not to any great extent possess the power of sprouting from the stump, at least in this region.

A similar situation was noted in a narrow valley near Duncan Bay (sec. 28, T. 67 N., R. 33 W.), which was protected by abrupt ridges on both sides. Here the trees of all species are very large, the shade is not dense, and windfalls are relatively scarce. Ground hemlock is exceedingly abundant and large, and is plainly responsible for the lack of young tree growth and the resulting openness of the forest. Some scattered groups of small balsams were plainly related to windfalls.

The foregoing studies show that the climax forest is a complex of windfall areas of differing ages, the youngest made up of dense clumps of small trees, and the oldest containing a few mature trees with little or no young growth beneath, those of a single group being approximately even-aged. This mosaic or patchwork changes continually in a manner that may almost be called kaleidoscopic when long periods of time are considered. The forest as a whole, however, remains the same, the changes in various parts balancing each other.

EXTENT OF THIS TYPE OF FOREST AS THE CLIMAX OUTSIDE OF ISLE ROYALE

Attempts to obtain information relating to the nature of the climax forest of other portions of the northeastern conifer region have not been attended with much success. The distributions of the various trees have been determined by BELL (**8**) and others with considerable accuracy, but practically nothing of an ecological nature has been published. From the data I have been able to

discover, the impression has been gained that the same association of balsam, paper birch, and white spruce, which is the dominant forest type of Isle Royale, is found in the most mesophytic habitats throughout northeastern Canada. The probability is that it is the climax type over much of the region, though there is not sufficient evidence to justify a confident statement to that effect. It is not necessary that the component species bear the same relations to each other in all parts of the region, or even that the species themselves be everywhere the same. One or even two of the climax trees may be lacking in certain places, species that are ecologically equivalent may be substituted, or others added. Analogous differences occur in the deciduous forest. The two climax trees that are almost omnipresent are the maple and the beech, and yet there is a belt along the northern edge of the region where the maple alone forms the climax forest, unless the yellow birch (*Betula lutea*) may possibly take the place of the beech. Again, in the Great Lakes region a third climax tree, the hemlock (*Thuja canadensis*) is present; and in the southern Appalachians the number of species composing the climax forest reaches a dozen or more. Similarly, in northeastern Canada the climax forest may vary from place to place.

Of northern Quebec MACOUN (**39**) says: "In the country around Lake Mistassini it [balsam] grows mixed with aspen, birch, and white spruce, and on the lower part of the Rupert River it is found growing with the same trees all the way to James Bay." The correspondence of this to the Isle Royale forest is striking. In reports of the Department of Lands and Forests of Quebec (**45, 46**) expressions such as the following are frequent, the region described being the country north of Lake St. John, west to Lake Abitibi: "well timbered, mostly with spruce, fir, and white birch, with some scattered white and Banksian pine on the high ridges." In the "Report of the survey and exploration of northern Ontario" (**43**) there is much detailed information concerning the distribution of the trees in that region, though the data presented have little ecological value. However, in reading the reports of the various parties one frequently comes upon such statements as the following: "chiefly small poplar [*Populus tremuloides*], spruce, white birch,

and balsam, and a few balm of Gilead [*Populus balsamifera*]"; "spruce, balm of Gilead, poplar, balsam, and white birch"; "white birch, balsam, and a few large spruce"; "the white variety of spruce of good size was seen continually along the rivers and on

FIG. 14.—Ranges of the climax trees of the northeastern conifer forest and the eastern deciduous forest.

ridges back from them. Black spruce, generally scrubby, clothes the muskegs. . . . . Birch and balsam are also common on high lands." The black and white spruces are not usually distinguished in these reports, but it is clear that the former is the principal tree upon the extensive muskeg lands, while the latter is confined to the

higher grounds, where it usually has the balsam and birch as its companions.

The data here presented, though very unsatisfactory, are sufficient in my opinion to establish the probability of the generalization that the climax type of the whole of the northeastern conifer region is of the general character described for Isle Royale, with local variations due to the elimination or addition of species, or to the substitution of others that are ecological equivalents.

Important confirmation has recently been received from Dr. ROBERT BELL of Ottawa, the best authority upon the distribution of Canadian trees, who writes: "The same type of upland forest which you describe on Isle Royale extends from the Great Lakes to James Bay and east and west of it, with modifications in parts."

On the map (fig. 14) the area shaded with oblique lines represents the region over which the ranges of the balsam, paper birch, and white spruce overlap, *north* of the range of the sugar maple (data largely from TRANSEAU **55**). It is in this region that the type of forest described is thought to be the climax. Beyond the limits of the balsam, which has the narrowest range of the three, some other species must be substituted for it, or else the climax forest is composed of the remaining two species alone.

COMPARISON WITH THE CONIFER FOREST OF THE SOUTHERN APPALACHIAN SUMMITS

In connection with the study of the Isle Royale forest it will be worth while to make comparison with another region that has come under my observation, where the forest is extremely similar to that described in the present paper. On the highest summits of the mountains of North Carolina, eastern Tennessee, and southwestern Virginia, there are isolated areas of dominantly coniferous forest, which seem like detached portions of the great northeastern forest (see detailed description by HARSHBERGER **32**). The species are different, the balsam being *Abies Fraseri* (Pursh) Poir., the spruce *Picea rubra* (DuRoi) Dietr., and the birch *Betula lutea* Michx. f. In general aspect this forest is surprisingly like that of Isle Royale. Because of the predominance of the first tree mentioned many of the mountains themselves are locally called "Bal-

sams." The results of studies upon three of these summits in western North Carolina may be briefly summarized as follows, the localities being Richland Balsam, Plott Balsam, and the Black Mountains (Mount Mitchell).

The coniferous forest covers the mountain slopes from about 1600 m. to the summits, the highest of which is about 2010 m. *Abies Fraseri* is on the whole the most abundant species except along the lower edge of the coniferous region, where *Picea rubra* is of somewhat greater importance. *Betula lutea* is scattered more or less thickly throughout and grows to a great size, specimens having been noted that were 1.3 m. in diameter. As on Isle Royale, birch and spruce are sparsely represented in the young growth, which is predominantly balsam. The shrubby vegetation consists almost entirely of *Rhododendron catawbiense* Michx., which is very abundant. It is interesting to note that the balsam seedlings are practically absent under the shade of the rhododendrons, and scarce in shade in general, but are exceedingly abundant in partial openings. The ground is covered by a luxuriant moss carpet, almost identical in composition with that of the Isle Royale forest, and the herbaceous growth includes most of the characteristic group of northern forest plants which has been listed (p. 16).

The similarity between Isle Royale and the North Carolina "Balsams" is thus a striking one. In the latter region there is even an ecological equivalent to the ground hemlock. *Rhododendron catawbiense*, in spite of its very different habit, is equally effective in densely occupying and shading the ground and thus in temporarily preventing reproduction of the forest trees over wide areas. I believe that the conclusions which have been reached concerning the Isle Royale forest will also hold, with minor modifications, for the forests of the North Carolina summits. The conifer-birch forest of the mountains is to be regarded as the climax type of its own limited area (not including, of course, the lower slopes dominated by deciduous trees), and at the same time as an extension or outlier of the northeastern climax forest.

THE MAPLE FOREST OF ISLE ROYALE AND ITS RELATIONS

Wherever the sugar maple occurs it forms a part of the climax forest, and is usually the dominant species therein. Between the two great eastern forest regions there is a transitional belt several hundred kilometers wide where the three climax trees of the conifer, and the two of the deciduous forest all occur (see map, fig. 14). This belt extends from northern Wisconsin through the upper peninsula and the northern part of the southern peninsula of Michigan and eastward to New Brunswick. WHITFORD (**59**) studied the successions in a portion of this belt, and found that the climax forest in northern Michigan (both peninsulas) is the beech-maple type. The balsam, birch, and spruce are very abundant, but here they belong to preliminary stages in the successions. GANONG (**26, 27**) gives an excellent summary of the plant formations of New Brunswick. He states that the climatic forest type is the "mixed maple-birch-spruce-fir association." There is no indication in his paper that the maple ever supersedes the other trees, but the presence of such a possibility must be admitted. The conclusion from the studies of WHITFORD and others seems to be that the maple and beech, where not climatically excluded, are able to supersede the climax trees of the northeastern forest.

Coming now to Isle Royale, we find upon the southwestern end, occupying the summit of the highest ridge, a mixed growth of *Acer saccharum* Marsh (sugar maple), *Betula lutea* Michx. f. (yellow birch), and *B. lenta* L. (sweet birch); with the characteristically northern trees as a minor element (see ADAMS **4**, pp. 30–31, and HOLT **33**, p. 224). The maple is decidedly the dominant species and reaches a large size.[1] At the northern edge of this northernmost outpost of the maples we may draw the line that separates the true northern forest from the transitional belt (fig. 14). South of this line the representatives of the southeastern deciduous forest, though not necessarily forming the bulk of the stand, yet have the upper hand; north of it the supremacy of the conifers and the paper birch is undisputed.

[1] It is of interest to note that the maple is common on the southern side of Michipicoten Island, near the eastern shore of Lake Superior.

Since glacial times there has been a continual northward advance of the forest, with the conifers as the pioneers, closely followed by the hardwoods. The problem as to whether the extension of the latter is still going on might be studied to good advantage in such localities as the southwestern end of Isle Royale, and Michipicoten Island. The large size and thriftiness of the maple at its northernmost limit would seem to indicate that it has not reached its climatic limit (BELL 8). The manner and causes of "climatic successions," or the invasion of one climax forest by another, are still to be worked out.

SUMMARY.—THE CLIMAX FOREST

I. The dominant forest of Isle Royale is composed of *Abies balsamea*, *Betula alba* var. *papyrifera*, and *Picea canadensis*, with a few other species occasionally present. *Abies*, all sizes and ages considered, is by far the most abundant, but the greater number of individuals are small. *Betula*, although conspicuous, is not abundant, and young trees are scarce. *Picea* is rare, though occasional specimens tower high above the other trees. Shrubs and herbaceous growth are sparse except in partial openings. The most important element in the latter is the moss contingent, which is responsible for the formation of great amounts of humus.

II. Studies of individual species gave the following results. *Abies* is preponderant in the young growth because (1) the seedlings make a successful start in almost any situation provided sufficient light be available; (2) the species reproduces abundantly by layering. Its rapid decrease when greater size and age are considered is due to (1) competition because of abundant germination; (2) fungus attacks, and (3) brittleness of wood, both resulting in extreme liability to windfall. Its high birth-rate is balanced by a high rate of mortality. *Betula* does not germinate abundantly in the forest, but, because it is not liable to disease and windfall, holds its own with *Abies*. Even when broken off by severe winds it has a means of recovery in its ability to produce stump sprouts. Its more rapid growth gives it an advantage in competition with *Abies*. Abundant light is necessary for successful reproduction. Low birth-rate is compensated by a very low mortality. *Picea* is

ecologically unimportant on account of its scarcity. Germination in the forest is less abundant than in the case of *Betula*. It is not liable to fungus attacks and withstands severe winds. Birth-rate and mortality are both low. *Taxus canadensis* is the most important species of the undergrowth, its influence lying in the completeness with which it occupies and shades the ground, preventing tree reproduction over large areas.

III. Intensive study of selected areas (quadrats) yielded the following facts concerning the dynamics of the forest.

The forest is a complex of windfall areas of differing ages, the youngest made up of dense clumps of small trees, and the oldest containing a few mature trees with little young growth beneath. The history of a windfall area is as follows. After the débris has disintegrated sufficiently to allow abundant light to reach the ground, a new generation of trees springs up, approximately even-aged, composed of the three dominant species, *Abies* always greatly preponderant. During the continued development of this group most of the individuals are at various times eliminated, *Abies* suffering most for the causes enumerated in section II. Because of the dense shade no new individuals can start beneath them, and the final outcome is a group composed of a few large trees, approximately even-aged, in which *Abies* has nearly or quite lost its position of dominance to *Betula*. In situations sheltered from wind all species live to a greater age and windfalls are less frequent. The processes though less rapid are nevertheless the same as in more exposed situations. The result in the forest in general is a mosaic or patchwork which is in a state of continual change. The forest as a whole remains the same, the changes in various parts balancing each other.

IV. The following evidences that the dominant forest of Isle Royale is also the climax have been derived from the studies summarized above and from those dealing with the successions.

1. The dominant forest is the most mesophytic of the plant societies.

2. It is uniform upon all soils and upon areas that have passed through very different lengths of subaerial history.

3. All the successions culminate in the establishment of this as the final stage.

4. The character of the forest as a whole is stable, though any given area is continually changing in composition and relative proportions of the various species.

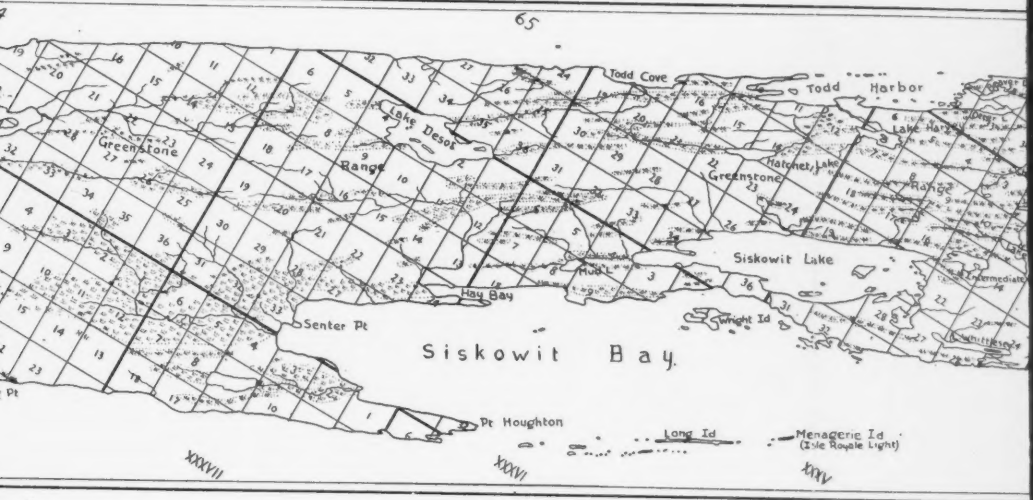
V. The same type of forest, with local differences in some places, is probably the climax throughout the northeastern conifer region.

VI. Comparison with the conifer-birch forest of the southern Appalachian summits shows a striking equivalence of species and marked correspondence between the two in ecological characteristics, indicating that the forest dynamics are essentially the same. The mountain forest may logically be considered as a southward extension or outlier of the northeastern climax forest.

VII. *Acer saccharum* is dominant upon the main ridge at the southwestern end of Isle Royale, reaching here its extreme northern limit in this region. Southward it is probably able to supersede the conifers and birch, while north of its northern limit the supremacy of the latter trees is undisputed.

PALO ALTO, CALIFORNIA

XXXVIII


Todd Cove
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Lake Desor
Greenstone
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Hatchet Lake
Greenstone
Range
Siskowit Lake
Hay Bay
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Wright Id
Siskowit Bay
Pt Houghton
Long Id
Menagerie Id
(Isle Royale Light)
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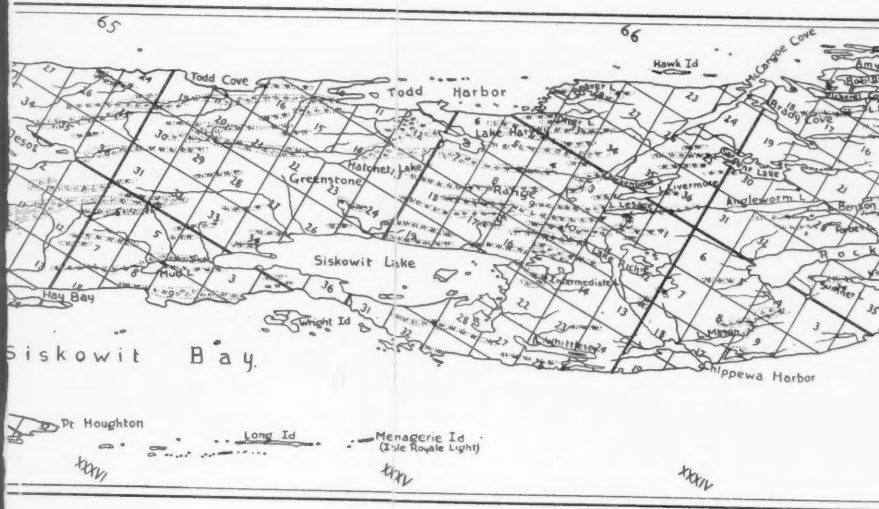
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Todd Cove
Todd Harbor
Hawk Id
McCargoe Cove
Lake Harbor
Greenstone Ridge
Hatchet Lake
Siskowit Lake
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Pt Houghton
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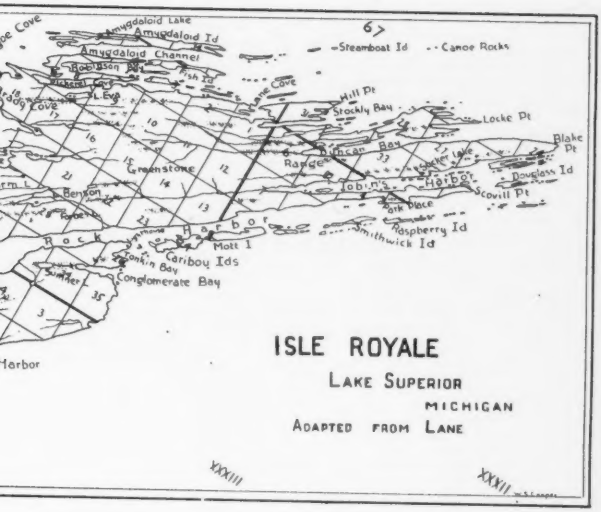
67
Amygdaloid Lake
Amygdaloid Id
Amygdaloid Channel
Steamboat Id
Canoe Rocks
Hill Pt
Stockly Bay
Locke Pt
Blake Pt
Rangers
Tobin's Harbor
Douglass Id
Scovill Pt
Raspberry Id
Smithwick Id
Mott I
Caribou Ids
Conglomerate Bay
Greenstone
Harbor
ISLE ROYALE
LAKE SUPERIOR
MICHIGAN
ADAPTED FROM LANE
XXXIII
XXXII

PROGRESSIVE AND RETROGRESSIVE CHANGES IN THE PLANT ASSOCIATIONS OF THE DELAWARE COAST

LAETITIA M. SNOW

(WITH SIX FIGURES)

During July and August 1901, certain observations were made on the plant associations of the Delaware coast, from Cape Henlopen southward, for about six miles.[1] Ten years later, in July 1911, the same region was again visited in order to ascertain the changes which had occurred during the interim.

Considering the extreme instability of dune topography, surprisingly little change was noted, thus indicating the slowness with which plant associations, in general, change their character. Certain observations, however, seem of value, as indicating the direction of change in various associations, and are therefore recorded.

As in the previous study, on account of the lack of flowers and fruit, the identity of many forms was difficult—at times impossible—to determine. For regions which showed practically no change, no lists are presented. Where changes were noted, only dominant forms are given, in order that an idea of the direction of change may be obtained. The nomenclature of GRAY'S *Manual* (7th edition) is used, with the BRITTON synonyms in parentheses.

Grateful acknowledgment is due Professor KARL M. WIEGAND for his kind assistance in the identification of certain species.

I. Geography and physiography

As a general discussion of the position, topography, soil, and climate of the region was presented in the former paper, a consideration of these points will be omitted.

II. Plant formations

A. TREELESS OPEN

1. *Beach formation.*—(*a*) *Lower beach.*—The contour of the lower beach varied exceedingly during July 1911, thus indicating

[1] SNOW, L. M., Some notes on the ecology of the Delaware coast. BOT. GAZ. 34: 284–306. *map* and *figs. 1–10.* 1902.

an unstable condition. This instability is further evidenced by the fact that, during the 20–25 years which have elapsed since some of the summer residents first visited the region, the beach and the sea-cliff, along which Surf Avenue extends, have receded many feet. After great storms, especially during the winter, the beach is said to be several feet lower, exposing at such times ledges of peaty material. During the period of this study one small ledge nearly in front of Hotel Henlopen, Rehoboth, was twice exposed,

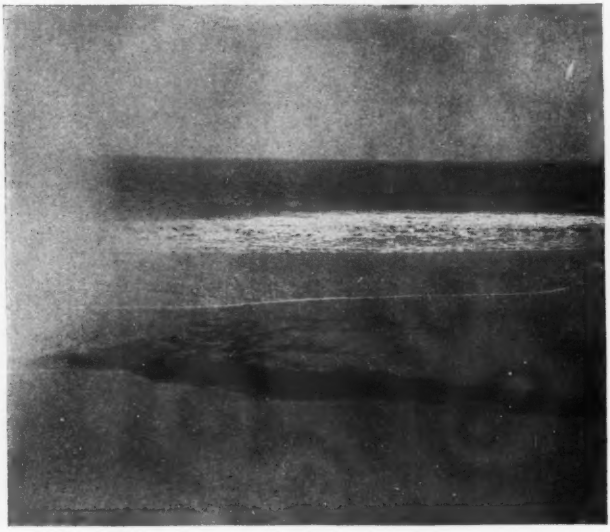

FIG. 1.—Ledge of peat in the beach near Henlopen Hotel, Rehoboth, Del.

appearing somewhat as in fig. 1. It is said to underlie the coast from Rehoboth to the Henlopen Life Saving Station. One fisherman reported that in winter a ridge of "turf with stumps in it" is exposed in the beach opposite Delaware Avenue. Reference to similar beach-buried peat is made in the report of the Intercollegiate Geological Excursion, 1911.[2]

b) *Middle and upper beaches.*—As was noted in the former paper, no upper beach can be distinguished. This year there is

[2] The Intercollegiate Geological Excursion. Science N.S. 34:611–614. 1911.

pratically no middle beach, the summer storm-tides usually reaching the bases of the frontal dunes. The succulents characteristic of this zone appear, therefore, around the bases and on the slopes of these dunes.

2. *Dunes.—Outer series.*—This series is practically fixed from the Henlopen Life Saving Station to a similar station at Dewey Beach, a distance of five miles. The dunes are held chiefly by *Ammophila arenaria*, with a sprinkling of *Cenchrus tribuloides* and succulents.

Between these dunes are many passages leading into hollows or lakes which are flooded in times of storm. As the beach is narrowing, the flooding of these regions occurs more frequently than formerly, thus causing a retrogression toward more hydrophytic conditions.[3] The best example of this is the "flooded area" north of Rehoboth, called in the previous paper "desert waste," because a large portion of it was at that time bare, damp soil. It is reported to be at times "dry with a shining crust," but in July 1911, although the month was a rather dry one, the whole area appeared to be under water, thus indicating a greater inflow from the sea. At the south edge of this region are to be found isolated plants of *Mollugo verticillata*, *Sesuvium maritimum*, and *Spergularia marina* (*Tissa marina*). A second example of flooding by the sea is presented by Silver Lake, south of Rehoboth. The presence of numbers of crabs in this lake indicates frequent additions of salt water. This inflow of the sea takes place at a point near the south end of the lake where the margin closely approaches the tide line. Similar retrogressive movements have been described by HARSHBERGER as occurring in northern New Jersey.[4]

As was formerly noted, a region of great activity extends from a short distance south of the Henlopen Life Saving Station to the Henlopen Lighthouse. The large dunes, forming three amphitheaters opening seaward, have moved many feet inland during the last ten years. In passing back over alternating pine ridges and swamps, they have exposed "pine graveyards" and left in

[3] COWLES, H. C., The causes of vegetative cycles. BOT. GAZ. **51**:161–183. 1911.

[4] HARSHBERGER, J. W., The vegetation of salt marshes, and of salt and fresh-water ponds of Northern Coastal New Jersey. Proc. Acad. Nat. Sci. Phila. 1909:373–400. *figs. 1–6.*

their seaward hollows swamps and ponds, which are at times flooded by the tide. In the third of these amphitheaters (fig. 2) many slabs of peat may be seen, which have probably been washed inland from the ledge below tide line.

Across the cape extends the long dune upon which stands the Henlopen Light. This is the largest dune in the region, estimated ten years ago to be 80–90 ft., when the crest was at the lighthouse. By 1911 the summit had moved about 300 ft. to the southwest, and

FIG. 2.—View from the crest of the lighthouse dune, looking south over the third amphitheater; flooded area in the distance.

appeared to be several feet higher than the base of the lighthouse. This advance has not changed the general appearance of the region, as photographs taken from the same points on both visits are very nearly identical. In spite of the fact that this is an active dune, a small clump of *Ammophila* has managed to gain a foothold on the crest (fig. 4).

The appearance of the cape after ten years is apparently unchanged. A low beach extends around the point, bordered on the inner side by low dunes, which inclose a complex of dunes and

swamps. A few shrubs appear on the dunes and a low ridge bearing small trees nearly crosses the cape, as may be seen in fig. 5.

South of Rehoboth the edge of the frontal ridge of dunes passes into a rolling plain called "a heath," and, although the growth of the shrubs and stunted trees gives the region a more thicket-like appearance, the flora has apparently not materially changed.

3. *Hudsonia complex.*—North of Rehoboth may still be found the region called a "*Hudsonia* complex," a jumble of small dunes,

FIG. 3.—Eroded face of the lighthouse dune; view taken from the northeast slope.

held principally by *Hudsonia tomentosa*, with swamps occupying the depressions between them. The flora of these dunes exhibits a more heathlike character than it showed ten years ago. South of Rehoboth the drying of the *Hudsonia* complex has progressed still farther. Swamps are rather rare, remnants showing in places, where *Scirpus americanus*(?) and *Juncus* sp. give evidence of former swampy conditions.

4. *Swamps and meadows.*—As the flora around Silver Lake was studied somewhat more in detail ten years ago than that of the

other meadows, it would have been interesting to have made careful comparisons this year. But unfortunately that region has been converted into a pasture, and is closely grazed. The few forms found in the fence corners, however, indicate an assemblage similar to that occupying this region ten years ago. As one passes northward the flora changes, many more heath forms appearing this year than at the time of the previous study. This seems to indicate that the higher land has become drier, while the land in lower

FIG. 4.—View from the top of the lighthouse looking southwest; this figure is a continuation to the right of fig. 2.

situations has maintained its swampy meadow character, due to the frequent additions of sea water to the lake.

North of Rehoboth, around Frazer's Lake, there extends a large swamp. Near the lake the cat-tail is apparently the dominant form, while to the east and north this association passes into a meadow which is a second pasture. This swampy meadow extends to the flooded area on the north and has a very uniform appearance. Only the southeastern extension, as it runs between the *Hudsonia* dunes, was studied. Many typical undrained swamp forms were

listed, among which may be noted *Spiranthes praecox?* (*Gyrostachys linearis?*), *Viola lanceolata*, *Juncus scirpoides*, *Osmunda regalis* (*O. spectabilis*), and *Aspidium Thelypteris* (*Dryopteris Thelypteris*).

In the *Hudsonia* complex, as previously noted, are many small swamps. The segregation of species in these swamps is most singular. Neighboring hollows may have almost totally different associations. One may be carpeted with cranberries, while in another, a few feet away, not a plant of this species is to be

FIG. 5.—View taken from the top of the lighthouse looking north across the cape; Delaware Bay to the left; the Atlantic Ocean to the right.

found. The hollows appear to be remnants of the south end of the swampy meadow around Frazer's Lake, and, with the lake, apparently are not affected by the tidal inflow, which seems to reach only the northern end of the meadow. The hollows and the lake, therefore, show progressive changes.

One easily identified pine swamp was rather carefully studied in 1901 and again in 1911, with the following result: *Osmunda regalis*, *Aspidium Thelypteris*, *Vaccinium macrocarpon* (*Oxycoccus macrocarpon*), *Xyris flexuosa*, *Rhexia virginica*, and *Smilax rotundi-*

folia have disappeared; while *Lyonia ligustrum* (*Xolisma ligustrum*), *Ascyrum hypericoides*, *Eupatorium hyssopifolium*, *Rubus* sp., *Vaccinium atrococcum*, *Gaylussacia baccata* (*G. resinosa*), *Baptisia tinctoria*, *Rhus Toxicodendron* (*R. radicans*), and *Quercus marylandica* have established themselves.

No sphagnum has been found, and none could be identified in the peat collected. The absence of typical peat bogs from the eastern shore of Maryland was noted by SHREVE,[5] although sphagnum was found abundantly in the clay upland swamps.

Hibiscus Moscheutos has apparently disappeared from these hollows in the ten-year interval, but whether this is due to the stress of changing ecological conditions or to the assiduous gathering of the plants cannot be stated.

5. *Heath.*—This formation shows a progression toward the development of a forest by a greater growth of the shrubs and trees, without much change from a floristic standpoint.

B. WOODED REGION

The thicket and forest formations have received no detailed study at either time, but the collections made this year indicate that the pine stage, represented by *Pinus Taeda* and *P. rigida*, is being succeeded by the oak-hickory stage, represented by young plants of *Quercus marylandica*, *Q. alba*, *Q. velutina*, *Q. stellata* (*Q. minor*), *Q. falcata* (*Q. digitata*), *Carya glabra* (*Hicoria glabra*), and *C. alba* (*H. alba*). The list of associated forms is incomplete, but it is interesting to note that the species found are not those characteristic of similar situations in New Jersey or southward,[6] but that many of the plants found in clay and sandy loam areas of the Talbot terrace of Maryland are present (SHREVE *loc. cit.*). According to the manuals, the northern limit of *Myrica cerifera*, a typical pine barren plant, is Maryland. It was found, however, at Rehoboth and is mentioned by STONE[7] as occurring in the southern

[5] SHREVE, F., The plant life of Maryland. Md. Weather Service, Spec. Publ. III. 1910.

[6] HARPER, R. M., Science **25**:539–541. 1907.

[7] STONE, WITMER, The plants of southern New Jersey. Rep. N.J. State Museum. 1910.

part of New Jersey. I agree with STONE (*loc. cit.*), SHREVE (*loc. cit.*), HARPER,[8] and WILLIAMSON[9] that the flora of southeastern Delaware has affinities, southward and northward, with districts much farther inland, rather than with the coastal regions.

C. THE CANAL DUNE

This dune, mentioned in the previous paper as having been formed, about a mile inland, from material excavated in making a canal, is at this time practically fixed. This is due (1) to the fact that the finer sand has been blown away, leaving the coarser material, and (2) to the binding power of plants. No *Ammophila* is to be found, but many of the plants characteristic of the *Hudsonia* complex and of the heath are present.

III. Problems connected with the region

Second series of dunes.—This series was omitted from the foregoing discussion, because of its possible relation to the problem concerning the change in direction of the coast line.

This ridge of dunes is best seen north of Rehoboth, extending to the northwest from the end of the board walk, thus making an angle with the coast. It was considered in the previous report (p. 286) to be a ridge of dunes blown from the coast in a southwesterly direction. The dunes lie on a hard, flat foundation of clay and sand impregnated with iron. This is continuous with the bluff along which Surf Avenue lies and with the clay-sand ledge south of the town, shown in fig. 6. A portion of this ledge was figured in the previous paper (p. 285) and erroneously called sandstone. At Dewey Beach there again appears a clay-sand ledge, crowned with dunes, which, taken in connection with the clay areas north of Silver Lake, may be a continuation of the same formation. In the absence of any geological information on the subject, the fact that these various outcroppings appear to be at the same level, together with their probable connection, suggests the possibility that this low bluff was the original sea-cliff, running from

[8] HARPER, R. M., Car-window notes on the vegetation of the Delaware peninsula and southern Virginia. Torreya **9**: 217–226. 1909.

[9] WILLIAMSON, C. S., Notes on the flora of central and southern Delaware. Torreya **9**: 160–166. 1909.

Dewey Beach to Rehoboth roughly parallel with the present coast, and north of Rehoboth extending in a northwesterly direction. There are many irregularities in this line, now occupied by lakes, streams, and marshes, which suggest erosion of the cliff.

The second interesting problem is connected with the plant remains, which in a thick peaty mass apparently underlie a large part of the present beach. This deposit was undoubtedly formed in a swamp, which would indicate that at one time the coast line

FIG. 6.—Clay-sand ledge south of Rehoboth, Del.; view from near the end of the board walk looking south; Dewey Beach in the distance.

was *farther out*. The following history seems reasonable and is suggested as a possible explanation. The sea-cliff stage was followed by the formation of a bar to seaward, inclosing a lagoon, which by progressive changes became a swamp. That the swamp stage must have continued for some time is suggested by the report of "stumps in the turf." Erosion of the seaward side of the bar followed, involving the driving backward of the dunes over the swamp and the formation of a hook at the north end of the bar,

thus extending the coast northward with the development of Cape Henlopen. This erosion stage is still in progress.

IV. Summary

1. Ten years is too brief a period in which to show any considerable change in plant associations, even in so active a region as that of the dunes.

2. Progressive changes were observed: (a) advancement of the *Hudsonia* complex toward the heath; (b) advancement of the heath toward the thicket; (c) drying of isolated swamps and lakes; (d) fixation of the "canal dune."

3. Retrogressive changes were noted: (a) recession of the coast, resulting in more frequent flooding of certain regions, thus continuing or increasing their hydrophytic character; (b) movement of active dunes over the forest.

4. The character and position of the sand-clay ledge suggests that it may have been an ancient sea-cliff.

5. The presence of a ledge of peat in the beach indicates the location of a former swamp.

6. This swamp was probably due to the presence of an ancient bar inclosing a lagoon.

7. The present erosion of the coast indicates that this bar with its dunes was moved inland over the swamp, while portions of the beach material were carried northward to form the hook.

8. This process of erosion is still in progress.

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RAY TRACHEIDS IN THE CONIFERALES[1]

RUTH HOLDEN

(WITH PLATES I AND II)

In classifying the various families of conifers from an anatomical standpoint, the structure of the medullary rays, whether fusiform or linear, thin or thick-walled, pitted or unpitted, has been a valuable criterion. Another feature which has not been emphasized as much as it deserves is the presence or absence of ray tracheids. DEBARY, MAYR, PENHALLOW, and others have reported them in certain genera, but to reach any conclusion of phylogenetic importance it will be necessary to consider the conditions affecting their appearance in all the main groups of conifers, extinct as well as living.

Extinct conifers

Succiniferous *Pityoxyla* of the Lower Cretaceous as described by JEFFREY and CHRYSLER (1) lack ray tracheids of any sort. In another less ancient cretaceous *Pityoxylon*, described by BAILEY (2), however, ray tracheids are present, both marginal and interspersed. Likewise in amber containing *Pityoxyla* from the Baltic deposits of the Late Eocene or Early Oligocene (3), marginal tracheids are present in the mature wood, though not in the early annual rings. In other types of fossil wood, namely *Cupressinoxylon*, *Cedroxylon*, *Taxoxylon*, *Araucarioxylon*, etc., ray tracheids have not been described.

Living conifers

ABIETINEAE

JEFFREY (4) has divided the Abietineae into two groups: the Pineae (*Pinus*, *Picea*, *Larix*, and *Pseudotsuga*) and the Abieteae (*Abies*, *Cedrus*, *Tsuga*, and *Pseudolarix*). Ray tracheids are present normally in all four genera of the Pineae, attaining their greatest complication in the hard pines, where they are dentate and reticu-

[1] Contributions from the Phanerogamic Laboratories of Harvard University. No. 48.

late. Of the Abieteae, ray tracheids are present normally in *Cedrus* and *Tsuga*. DEBARY (**5**) and PENHALLOW (**6**) have both described them as characteristic of *Abies balsamea*, to which DEBARY adds *A. excelsa*, but as lacking in other species of *Abies*. More recently THOMPSON has investigated this genus (**7**) and found them absent invariably in normal wood, but recalled in a number of species as a result of injury. Curiously, he reports them lacking in *A. balsamea*, an observation which I have confirmed from a study of seedling, mature wood, vigorous branches, roots, cone axes, etc., wounded and unwounded. In *Pseudolarix*, also, I have been unable to find ray tracheids, even in severely wounded branches. *Pseudolarix*, however, seems to be a particularly unfavorable subject for the study of experimental morphology, traumatic resin canals being formed much less readily here than in the other members of the Abietineae. The only remaining genus, *Keteleeria*, has the wood structure of *Abies*. Ray tracheids are entirely absent even in such primitive regions as the first annual ring, cone-bearing branch, cone axis, and are not recalled after wounding, though there is an abundant formation of traumatic resin canals.

TAXODINEAE

The Taxodineae as a whole are simpler in wood structure than the Abietineae. The resin canals of the latter have disappeared here, except in *Sequoia* (**8**), their place being taken by resin cells. It would be natural to expect that the medullary rays also would be simpler, and this is indeed the case. The characteristically thick-walled, heavily pitted, parenchymatous ray cells of the Abietineae are replaced by thin-walled, sparingly pitted cells, and the ray tracheids characteristic of the Abietineae are lacking except under certain conditions to be described below.

The genus *Sequoia* undoubtedly stands nearest the Abietineae, since both living species have traumatic resin canals, and one fossil species (**9**), *S. Penhallowii*, has abundant pitting on the tangential walls of the ray cells, and crystals in the marginal cells like those of some species of *Abies*. Accordingly here if anywhere ray tracheids ought to be present, and GOTHAN has described them as of sporadic occurrence in the old wood of *S. gigantea* (**10**).

Fig. 1 represents a radial section of the wood of *S. gigantea;* fig. 2 a few cells of this ray at a greater magnification. Mixed with the typical parenchymatous ray cells, there are large square cells whose bordered pits on radial, tangential, and vertical walls prove them to be tracheids. This ray is unique, all others being composed of normal, horizontally elongated, parenchyma cells as shown in other parts of fig 1; and it is significant to note that the branch from which this section was cut had been badly wounded. This ray, however, occurred on the side of the branch opposite the wound, while the rays in the wound cap itself were perfectly normal. On examining other wounded specimens of *S. gigantea*, ray tracheids were found occasionally, always however in close proximity to the traumatic resin canals. All these other ray tracheids, moreover, were long and low, with bordered pits only on the horizontal wall next the parenchymatous ray cells.

Fig. 3 represents a ray from *S. sempervirens;* fig. 4 the same ray under a greater magnification. The ray tracheid here shown is like those commonly seen in *S. gigantea*, horizontally elongated, with bordered pits exclusively on the horizontal wall. Miss GORDON (**11**) has described ray tracheids in *S. sempervirens* and I have found them in every wounded piece examined, but not elsewhere. JEFFREY concluded from a study of resin canals that *S. gigantea* was more primitive than *S. sempervirens*, and the larger and more vigorous ray tracheids of the former corroborate his conclusion.

DEBARY has reported (**5**) ray tracheids in the monotypic genus *Sciadopitys*. My material consisted of a repeatedly wounded branch and possessed scattered ray tracheids of the type shown in fig. 5. Those described by DEBARY, however, were like those in hard pines, with "irregularly thickened ridges, projecting inward like teeth, on the upper and lower sides." The toothed cells I have seen were very rarely ray tracheids, but were rather of the nature of septate tracheids. Fig. 6 shows one of them.

Traumatic ray tracheids have been described by JEFFREY in *Cunninghamia sinensis* (**12**). It is interesting to note that he found them on the side of the branch opposite the wound, a condition like that mentioned above in *Sequoia gigantea.*

Specimens of *Taxodium distichum*, wounded and normal, of *Cryptomeria japonica*, and *Arthrotaxis selaginoides* were examined, but in none were ray tracheids observed.

Cupressineae

Of the genus *Chamaecyparis*, Penhallow (**6**) has described ray tracheids in *C. nootkatensis*, and absent elsewhere. In this species they are quite common, usually constituting the entire ray when one or two cells high, continuing for a time as such, and then becoming transformed into a parenchymatous ray. Careful examination, however, has revealed them in a number of other species. In *C. Lawsoniana* they are quite rare, but unquestionable. Fig. 7 shows their characteristic shape, long and low, with very small bordered pits next the parenchyma cells, two such pits being shown in the figure. *C. thyoides* and *C. plumosa* both show after injury tracheids of the same general appearance as those of *C. Lawsoniana*. A number of specimens of *C. pisifera* were examined before any ray tracheids were found. In one badly injured branch, however, there was a marked reversion to the thick-walled type of ray cell characteristic of the Abietineae, and between rows of these cells was a row of squarish tracheidal ray cells. In *C. obtusa* they seem entirely absent, even after injury.

In the closely allied genus *Cupressus* ray tracheids are much more common. Out of 7 species examined, they were present in 5; while of the other 2 species, only a small amount of material was available for study. The most frequent mode of occurrence is as an entire ray one to three cells high, though they have often been observed on the margin of higher rays. In this genus the relation to wounding is often diagrammatic. *C. guadalupensis*, after wounding, showed large numbers of ray tracheids. Fig. 8 shows a characteristic ray, but more commonly they constitute a ray one cell high, which soon turns into parenchyma; rarely they are marginal. *C. Macnabiana* presents the clearest case of traumatic reaction. Here frequently numbers of tracheidal rays one cell high start out immediately after a wound callus, extend through one or two years' growth, and then either die out or become transformed into parenchyma. *C. goveniana* showed the same

thing, but to a less marked extent. *C. macrocarpa* was less favorable, but in one slightly wounded branch a few ray tracheids were observed. In *C. Benthami* they are very rare, but the material examined consisted only of a seedling with no wounds. Similarly a seedling of *C. tortulosa* failed to show any, and in *C. occidentalis* they seem to be entirely absent.

The southern hemisphere genus *Callitris*, with its sub-genus *Tetraclinus*, has been described by BAKER (**13**) as entirely without ray tracheids. JEFFREY, however, observed them in *Callitris* in connection with the leaf trace, and I have seen them quite widely distributed, but always in small numbers. Throughout the genus they are invariably marginal, never standing alone. Fig. 9 represents a characteristic ray tracheid in *C. arborea*. Two lots of material of this species were examined, and the mature wood of both contained ray tracheids of this type. There seemed to be no relation to injury, for they were equally abundant inside and outside a wound callus. Small branches, however, in neither lot showed ray tracheids. Fig. 10 demonstrates the type of tracheid characteristic of *C. calcarata*. Here they are longer and lower than in the above-mentioned species, and, as there, the bordered pits are confined to the horizontal wall next the parenchyma cells. This material was entirely unwounded as far as could be seen. *C. columellaris* showed the same type of ray tracheids, even in normal tissue. *C. robusta* showed the largest number of tracheids of any species examined. They were present quite frequently in the mature wood, whether injured or not, but seem to be quite absent in the seedling stem. The ray tracheids are characteristically long and low, like those of *C. arborea*. *C. cupressoides*, as far as could be seen, lacks ray tracheids entirely, even in root wood. Fig. 11 shows a marginal tracheid in *Tetraclinus articulata*. They are present fairly abundantly in the mature wood, but are in general lacking in branches and twigs. One branch in which they were normally missing contained a few in the wound cap over a slight injury.

MAYR (**14**) has described ray tracheids in *Thuja plicata*, and I have found them quite common in both that species and in *T.*

occidentalis. Figs. 12 and 13 show a characteristic region of *T. occidentalis*. The tracheids are invariably marginal, with small bordered pits communicating with the parenchymatous ray cells, and slightly larger ones on their slanting end walls. *T. globosa* and *T. orientalis*, as far as examined, are entirely without ray tracheids, while in *T. dolobrata* they are rare.

PENHALLOW (**6**) has described ray tracheids in *Juniperus nana*, but states that they are lacking elsewhere in this genus. Wounds, however, in almost every species examined, sufficed to recall them. In *Juniperus* they occur usually as large, very irregularly shaped cells, thickly pitted on the tangential wall, constituting the whole of a ray one cell high. Rarely, also, they occur on the margin of parenchymatous rays, in which case the horizontal wall only is pitted. Fig. 14 shows a ray from *J. californica*. Ray tracheids have been observed in the following species: *J. californica*, *J. virginiana*, *J. pachyploea*, *J. scopulorum*, *J. occidentalis*, *J. chinensis*, *J. chinensis* var. *alba*, *J. sabina*, and *J. barbadensis*. In *J. communis* they were missing altogether from wounded seedling, stem, and root, except in the wound cap of one stem which had been repeatedly injured near the ground. Three species failed to show any: *J. bermudiana*, *J. californica* var. *utahensis*, and *J. macrocarpa*.

The genus *Libocedrus*, according to PENHALLOW, lacks ray tracheids. Figs. 15 and 16, however, show a ray of *Libocedrus decurrens* with a marginal tracheid. Toward the left of fig. 15 there is a bordered pit; fig. 16 shows it in greater magnification. This section was cut from wounded material, but other wounds examined failed to recall ray tracheids. Traumatic wood of *L. chilensis* and *L. doneana* seemed to be without them also.

Actinostrobus and *Fitzroya* (*F. Archeri* and *F. patagonica*) both lack ray tracheids, as far as investigated.

PODOCARPINEAE, TAXINEAE, AND ARAUCARINEAE

Saxegothaea, *Dacrydium*, *Podocarpus*, *Phyllocladus*, *Taxus*, *Torreya*, *Cephalotaxus*, *Araucaria*, and *Agathis* were examined, but no ray tracheids were observed.

Conclusions

To sum up, ray tracheids are present in *Pityoxyla* above the Middle Cretaceous; in all other fossil conifers they are absent. In living forms they occur normally in the Abietineae, traumatically in the Taxodineae and Cupressineae, but are invariably lacking in the Podocarpineae, Taxineae, and Araucarineae. Unless we are to assume that ray tracheids have developed independently in these groups, it is evident that the Taxodineae and Cupressineae must be related to the Abietineae. PENHALLOW admitted the relationship, but considered the cupressoid conifers ancestral to the Abietineae. The principle that traumatic tissue reverts to an ancestral type appears to be too strongly established to need discussion here. Applying this principle to the case in point, it must be seen that PENHALLOW has read the series in the wrong direction, and that the Taxodineae and Cupressineae are descended from rather than ancestral to the Abietineae. This conclusion might be questioned on the score that normally primitive regions, as first annual ring of seedling, root, cone axis, etc., fail to support the wound evidence by possessing ray tracheids. The answer to that appears to be simple: even *Pinus*, in which ray tracheids culminate, does not usually have them next the pith or in the cone axis. In other words, ray tracheids never made their way into the cone axis or first annual ring of any of the Abietineae, Taxodineae, or Cupressineae, but were characteristic only of mature wood. Consequently, now that they have become reduced in the last two families, they can be recalled only to the regions they once occupied normally. This conclusion as to the relative antiquity of the three groups, based on the distribution of ray tracheids alone, is corroborated by the conclusion reached by JEFFREY (**4** and **8**) from a study of resin canals.

The history of the development of ray tracheids, then, would be somewhat as follows. Up to the Middle Cretaceous, all *Pityoxyla* had simple medullary rays composed entirely of parenchyma. In the Middle Cretaceous they acquired ray tracheids. Some time between then and the Tertiary, a family sprung from these *Pityoxyla* characterized by the possession of ray tracheids. This family is the immediate ancestor of the Taxodineae and Cupressineae, while

the original *Pityoxylon* line has persisted to the present day as the Abietineae. In some of them ray tracheids have become more and more elaborated (hard pines); in others they have become reduced until they occur only traumautically (*Abies*) or are entirely lacking (*Pseudolarix*). In the Taxodineae and Cupressineae they have become more and more reduced until they are present normally in only a very few species, and traumatically in certain others.

Since the taxads, podocarps, and araucarians never have ray tracheids, it is evident that if they came off from the Abietineae, it must have been at some time before the Middle Cretaceous, probably in the early Mesozoic.

To this suggested Upper Cretaceous origin of the Taxodineae and Cupressineae, it might be objected that in the Lower Cretaceous and Jurassic there are present *Cupressinoxyla*, together with leafy twigs, cone scales, cones, etc., which have been referred to *Sequoia* and allied forms. There is however nothing to prove that these woods belong to the Taxodineae or Cupressineae rather than to the podocarps or taxads, which, as pointed out above, probably originated very early in the Mesozoic. As to the twigs, cones, etc., wherever it has been possible to investigate their anatomy, they have been shown to be araucarians and not *Sequoia* at all (**15** and **16**).

Summary

1. Ray tracheids are present normally in *Pityoxyla* from the Middle Cretaceous on, and in the Abietineae.

2. Ray tracheids are present traumatically in the Taxodineae and the Cupressineae.

3. On the evidence of traumatic recapitulation of ancestral characteristics, it is evident that the Taxodineae and Cupressineae are descended from the Abietineae, having sprung from that line at some time after the Middle Cretaceous.

4. Since ray tracheids are universally absent in the Podocarpineae, Taxineae, and Araucarineae, these lines must have come off from the Abietineae at some time before the Middle Cretaceous.

5. These conclusions are corroborated by a study of geological records and of other anatomical structures, as resin canals, wood parenchyma, etc.

I wish to express to Dr. E. C. JEFFREY my thanks for material and for advice throughout the course of this investigation, and to Mr. W. P. THOMPSON, Mr. A. J. EAMES, and Mr. E. W. SINNOTT for material.

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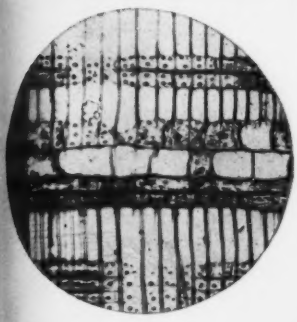

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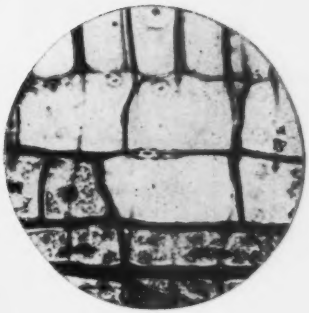

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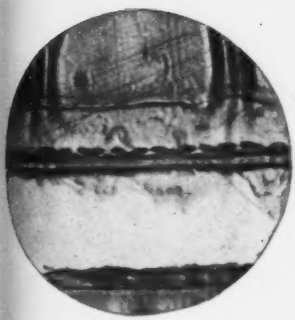

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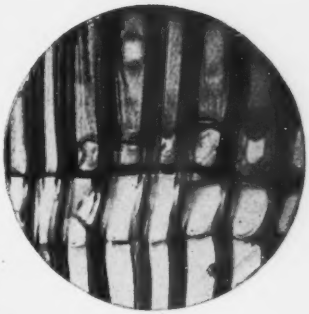

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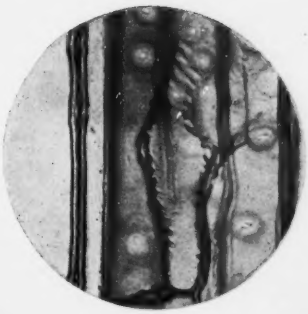

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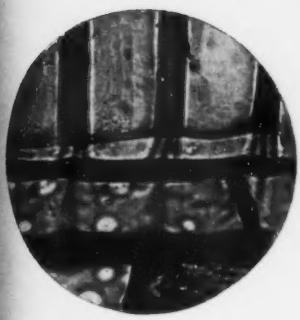

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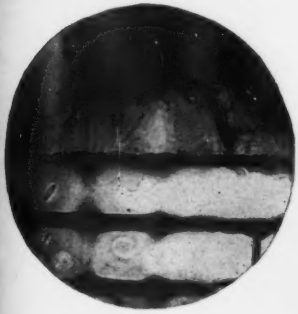
HOLDEN on RAY TRACHEIDS



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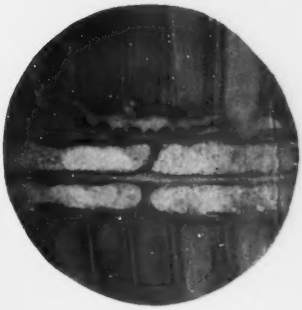

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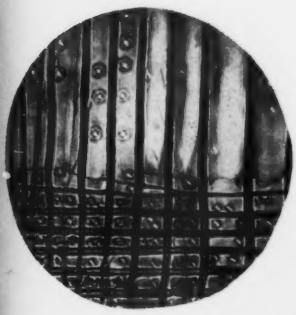

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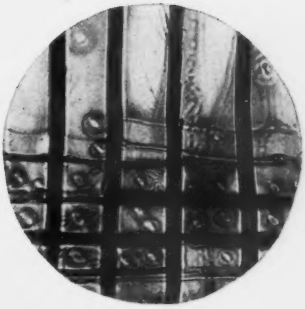

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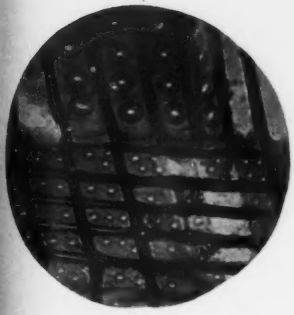

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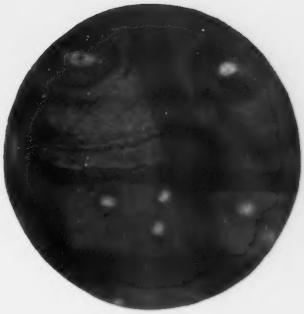

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HOLDEN on RAY TRACHEIDS

EXPLANATION OF PLATES I AND II

FIG. 1.—*Sequoia gigantea;* ×250.
FIG. 2.—Same; ×500.
FIG. 3.—*Sequoia sempervirens;* ×200.
FIG. 4.—Same; ×600.
FIG. 5.—*Sciadopitys;* ×400.
FIG. 6.—Same; ×600.
FIG. 7.—*Chamaecyparis Lawsoniana;* ×700.
FIG. 8.—*Cupressus guadalupensis;* ×600.
FIG. 9.—*Callitris arborea;* ×600.
FIG. 10.—*Callitris calcarata;* ×600.
FIG. 11.—*Tetraclinus articulata;* ×600.
FIG. 12.—*Thuja occidentalis;* ×200.
FIG. 13.—Same; ×700.
FIG. 14.—*Juniperus californica;* ×600.
FIG. 15.—*Libocedrus decurrens;* ×200.
FIG. 16.—Same; ×700.

THE LIFE HISTORY OF GLOEOTAENIUM

EDGAR N. TRANSEAU

(WITH PLATE III)

This peculiar alga was first collected by LOITLESBERGER at Ischl, Austria. On the basis of that material, HANSGIRG in 1890 described the genus and only known species, naming it for the collector, *Gloeotaenium Loitlesbergerianum* (1). He characterized the 2 and 4-celled families, with their encircling black bands. The chromatophore was stated to be star-shaped with a large central pyrenoid, and reproduction was limited to the multiplication by separation into two families. He thought the alga to be related to the desmids, and placed it together with *Spirotaenia* in a new family, the Pseudodesmidiaceae, which he conceived to be intermediate between the Desmidiaceae and the Palmellaceae.

In 1891 STOCKMAYER published a more detailed account (2) of the structure and life history, also based on a part of the material collected by LOITLESBERGER. He figures the 2 and 4-celled families and what he took to be a 1-celled individual. His 1-celled form, however, was either a diseased specimen or some other alga. The black band is described as originating by the gelatinization of the next to the outer layer of the mother cell wall in the plane of division. As gelatinization proceeds, the band is pushed inward until it occupies a position between the daughter cells. This process is preceded by the cell division and takes place about the same time that the outer gelatinous wall of the mother cell disappears. Gelatinous "caps" then develop near the poles of the mother cell, and as the second division takes place, these caps elongate in the plane of the second division until they fuse with the black band already formed. Inasmuch as polar "caps" also appeared in the 4-celled families, the author suggested the possibility of 8-celled families.

STOCKMAYER made it evident that the plant is not at all related to the Desmidiaceae, and that the black bands are hardly of sufficient importance to warrant the making of a new family. He con-

cluded that it is most nearly related to *Oocystis* and *Nephrocytium* among the Protococcoideae.

WILLE (3) in 1892 included *Gloeotaenium* among the doubtful genera of the desmids in the *Natürlichen Pflanzenfamilien*.

TURNER (4) published WALLICH'S notes and figures of the plant from Eastern India in 1892. WEST has expressed some doubt as to the validity of this determination. I do not believe, however, that there can be the slightest doubt about the first four of his figures representing the 2-celled form. The other figures are questionable.

GUTWINSKI (5) figured the plant under the name of *Gloeocystis cincta* in his flora of Tarnopol, Austria.

DE TONI (6) corrected this name in 1895 and listed the localities in Austria, Italy, and East India in which *Gloeotaenium* had been found.

SCHMIDLE (7) reported the plant from Australia in 1896, and WEST (8) figured it in 1904 from the Island of Trinidad. In *The green algae of North America* COLLINS (9) reprinted one of STOCKMAYER'S figures and placed the genus near *Gloeocystis* among the Chaetophoraceae. Its occurrence, at Charleston, Ill., was reported by the writer (10) in 1911. In the recently issued supplement to the *Natürlichen Pflanzenfamilien*, WILLE places the genus next to *Pleurococcus* among the Pleurococcaceae.[1]

Gloeotaenium has been collected at three stations near Charleston, Ill.: the second pond west of the tile factory; Hodgen's pond; and the first pond west of the Big Four Railroad bridge across the Embarras River. All of these ponds are artificial. The first and second are a mile apart, and the third is about four miles east of the other two. Up to the present time the alga has been found only in collections from very definite areas in each of the ponds. In the tile factory pond it is the northeast corner, in Hodgen's pond the northwest corner, and in the Big Four pond the middle of the east side.

In the four years during which collections have been made from these habitats, no specimens have been recognized earlier than the

[1] Since this paper was written, *Gloeotaenium* has been reported by A. B. KLUGH from Colpitts Bay, Ontario (COLLINS, F. S., The green algae of North America, supplementary paper. Tufts Coll. Studies **3**: 95. 1912).

last week in June nor later than the last week in October. Its vegetative period, therefore, is about four months in this locality. Early in the summer of 1911 I started some cultures in small aquaria in the laboratory. These have now been under observation for seven months and have provided a valuable check on the field observations.

As shown in the accompanying figures, the mature plant occurs as 1-celled individuals, and as 2, 4, and 8-celled families. The 1-celled mature individual (fig. 5) is comparatively rare; it is spherical in form and may or may not retain parts of the outer gelatinous covering of the resting cell (figs. 1 and 3). The diameter of the outer wall averages 35 μ and of the cell 25 μ. The chromatophore is globose, parietal, comparatively thick, and may or may not contain a pyrenoid. In young cells the chromatophore is finely granular, in mature ones it is usually gorged with starch. The nucleus is centrally placed.

The 2-celled families are abundant and exhibit a great variety of forms. Some of these variations are shown in the figures. The mother cell wall may be nearly smooth and lenticular in form, or may be partially covered with a gelatinous secretion, or rarely may consist of two distinct layers, of which the inner one may be folded at the poles so that when viewed from the side it shows three ridges at either end (fig. 24). Except for the outermost wall, this last form closely resembles those from Australia. At the poles there are usually small "caps" formed of a tough gelatinous secretion. These appear to be secreted after the loss of the gelatinous covering of the resting stage. STOCKMAYER seems to have believed them to be on the inside of the mother wall, since he speaks of their fusion with the "bands" in the formation of the 4-celled families. I have not seen any specimens, however, in which this is the case.

The "caps" are regularly external to the mother wall and the "bands" are regularly internal. An appearance of an external band is sometimes made as in fig. 6, in which an equatorial ring of the gelatinous secretion, which surrounded the aplanospore wall during the rest period, remains.

The 2-celled families are 40–70 μ in length, 22–40 μ in breadth, and 20–30 μ in thickness. The cells are spherical, or depressed

globose, sometimes flattened on the inner side, and sometimes on the outer. Between the two cells there is usually a gray, brown, or black band (figs. 8 and 9) composed of a more or less tough granular gelatinous secretion. This substance is at first colorless (fig. 4) and darkens with age. The color is partly due to total refraction and partly to a pigment. When the band is absent the caps also are wanting (fig. 10), but the band may be present without the caps. The mother cell wall is retained until late maturity, that is, until a short time (probably one or two weeks) before the breaking up of the family. In some cases this implies an existence during three or four months, and for those most favorably situated for development about a month.

My earliest outdoor record for the late maturity and aplanospore stage (figs. 17 and 18) is July 21. The disappearance of the mother wall is probably coincident with a rather rapid increase in the diameter of the vegetative cells from an average of 20 μ to an average of 30 μ. The cells remain attached to the band for a short period, but finally break away from this by their continued enlargement also. This last separation is clearly not due to the gelatinization of either cell wall or the band as stated by most authors. This is shown by the fact that after separation the band usually exhibits a ragged transparent edge, or occasionally there remains attached to it a thin wall from which the cell has escaped by tearing along the line of juncture with the bands. At the time of separation the cells may be thick or thin-walled, and may have divided internally (fig. 18). The thin-walled aplanospores germinate very soon by enlarging and dividing. The thick-walled aplanospores secrete a further gelatinous covering (fig. 1) and go through a rest period. Those cells which have already divided before separation may continue development (in the summer) or become thick-walled, secrete a gelatinous covering, and go into a rest period (in late autumn).

The 4-celled families are of two distinct types: (1) those having the cells in the same plane; (2) those in which the cells have a tetrahedral arrangement. In both the vegetative cells are similar to those of the 2-celled families. The 4-celled families with the cells in one plane (figs. 12 and 13) are about as abundant as the

2-celled families in this locality. They vary in form from circular-lenticular (fig. 15) to elliptical-lenticular (fig. 11); from those having plane walls (fig. 14) to those having marked polar flattenings with a central ridge (fig. 16); from those with thick bands and caps to those entirely lacking the gelatinous secretion. When seen from the flat side, the bands when present are cruciform. They lie well within the mother wall, but may extend some distance beyond the cells (fig. 12). In the late maturity stage the mother wall is lost and the cells enlarge until they rather than the bands become the conspicuous feature (fig. 19). The cells may then separate at once or divide internally before separation (fig. 23). After separation of the aplanospores development or rest period follows as described under the 2-celled families. The tetrahedral 4-celled family (fig. 20) differs in having a close-fitting mother wall, in the necessarily different arrangement of the bands, and in the absence of polar caps. The life history is probably the same as for the preceding forms.

The 8-celled families are exceedingly rare. Out of the hundreds of specimens of the plant which I have examined from the collections and cultures, not more than a score of this type have been found. Of these there have been two forms about equally abundant: (1) those having the 8 cells arranged in the form of a cube with an edge 35–50 μ long, and (2) those with the 8 cells grouped more or less irregularly. These latter have in one or two instances resembled a cube that has been compressed so that the upper and lower faces are the shape of a rhombus.

These 8-celled families have a close-fitting mother cell wall until late maturity, when they are held only by the gelatinous bands. STOCKMAYER predicted the possibility of 8-celled families on the basis of the caps in the 4-celled forms, but he evidently had in mind families with 8 cells in the same plane.

The most important result of the cultures, however, has been to show that the mature colonies do not divide, that is, the 2-celled mature colonies do not form 4-celled colonies directly. When the bands are once formed they are permanent structures. Whether the family shall be 1-celled, 2-celled, 4-celled, or 8-celled is determined by the number of divisions that take place within the aplano-

spore. I have found a number of cases where the divisions have taken place before the cell left the family, and before the heavy gelatinous outer covering was secreted (figs. 18 and 23). But it is probable that in most instances this division takes place after the resting period (fig. 2), for most of the aplanospores which I have examined showed no division and 1-celled mature individuals are comparatively rare.

That the propagative cells from 2-celled families do not necessarily form 2-celled families is shown in fig. 18, in which one of the cells has divided twice, the other but once. The development of the bands may be clearly understood from fig. 4. After germination (fig. 3) begins, the cells assume a more and more spherical form. Accompanying this process is the gradual separation of the cells and the secretion of the gelatinous layer from the adjacent cell walls.

My experience with *Gloeotaenium* both in the field and in cultures is thus far against the probability of zoospore production. The extreme localization of the collecting places in the ponds; the fact that it is most abundant on the bottom, and is brought to the surface only through the rising of other algae; and the fact that in the laboratory aquaria it is found only on the bottom, all point to the absence of swimming spores during the period I have had the plant under observation.

In the light of the above observations I should put the plant among the Scenedesmaceae near the genus *Oocystis*. The present description of the genus will require modification as follows:

Cells globose or variously flattened, solitary or united in families of 2, 4, or 8 cells, with wide and distinctly lamellate cell walls; the mother cell wall is frequently ornamented with folds and gelatinous disks opposite the cells; a dark-colored gelatinous layer usually extends between the cells of a family; chromatophore globose, with or without a pyrenoid. Reproduction by aplanospores and daughter cells.

The writer is under obligations to Mr. FRANK S. COLLINS and Professor WILLIAM TRELEASE for the loan of literature.

CHARLESTON, ILL.

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EXPLANATION OF PLATE III

FIG. 1.—Aplanospore showing gelatinous secretion outside the cellulose wall; from culture; this and succeeding figures are from camera drawings.

FIG. 2.—Embryonic family about to enter resting period; from Hodgen's pond October 28, 1911; cell wall in optical section showing lamellae.

FIG. 3.—Germinating aplanospore; from culture.

FIG. 4.—Embryonic family showing early stage in the process of "band" formation; from Big Four pond July 10, 1911.

FIG. 5.—Mature one-celled individual; from Big Four pond July 10, 1911.

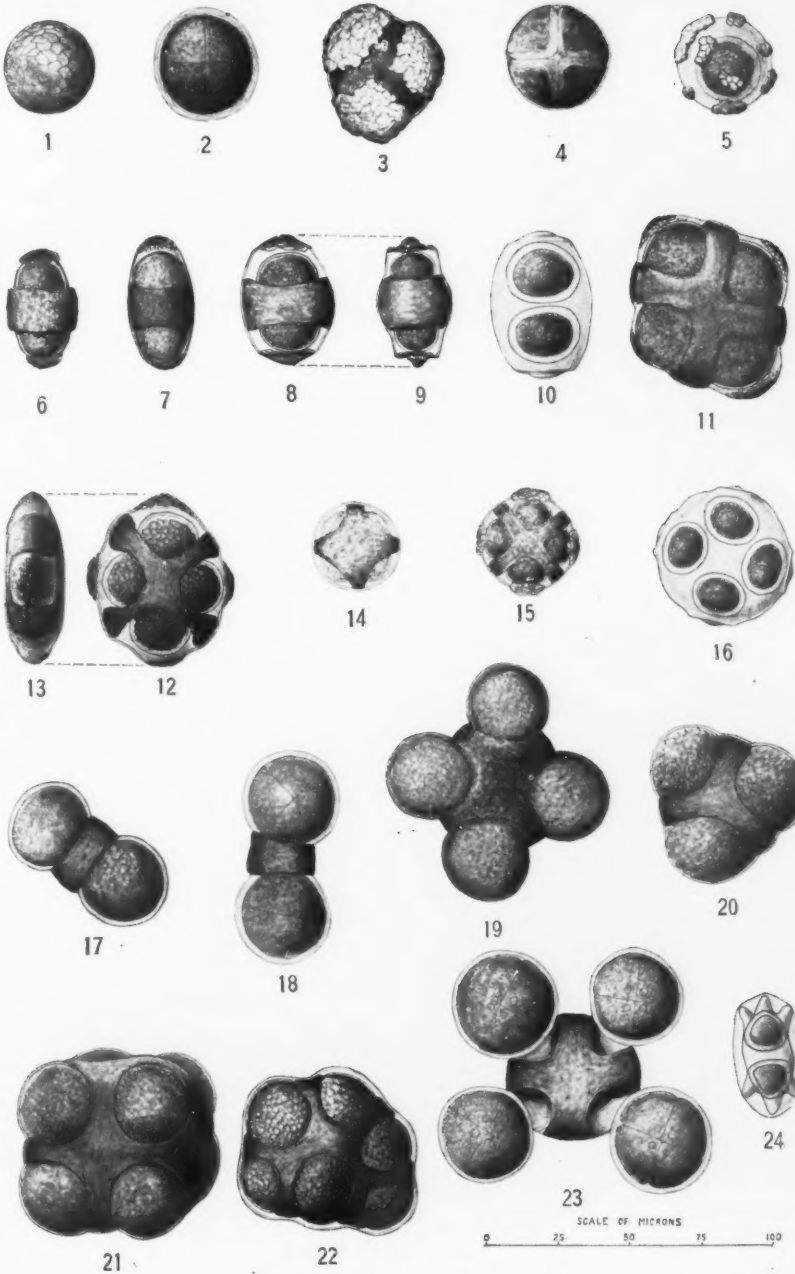
FIG. 6.—Two-celled family with equatorial remnant of gelatinous spore wall; from Hodgen's pond July 21, 1911.

FIG. 7.—Two-celled family showing band and caps; from Big Four pond July 10, 1911.

FIGS. 8 and 9.—Two-celled family, side and edge views, showing polar modification of the mother cell wall; from Big Four pond July 10, 1911.

FIG. 10.—Two-celled family lacking the gelatinous secretions; from Big Four pond July 10, 1911.

FIG. 11.—Four-celled family showing relation of bands and caps; from culture October 31, 1911.



TRANSEAU on GLOEOTAENIUM

FIGS. 12 and 13.—Four-celled family, side and edge views; from Hodgen's pond September 20, 1911.

FIGS. 14 and 15.—Young four-celled families; from culture July 25, 1911.

FIG. 16.—Four-celled family without gelatinous secretions.

FIG. 17.—Mature two-celled family; from culture October 10, 1911.

FIG. 18.—Contents of aplanospores dividing before separation.

FIG. 19.—Mature four-celled family; from Hodgen's pond July 21, 1911.

FIG. 20.—Tetrahedral four-celled family; from Hodgen's pond July 21, 1911.

FIG. 21.—Cubical eight-celled family; from Big Four pond July 10, 1911.

FIG. 22.—Irregular eight-celled family; from culture October 28, 1911.

FIG. 23.—Cells of four-celled family in which division has preceded separation; from culture October 28, 1911.

FIG. 24.—Double-walled two-celled family; from Big Four pond July 10, 1911.

HYDRODICTYON AFRICANUM, A NEW SPECIES

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 166

SHIGÉO YAMANOUCHI

(WITH SIX FIGURES)

The genus *Hydrodictyon*, as found in Europe, North America, and Asia, has been represented by a single species, *H. reticulatum* (L.) Lagerh. (*H. utriculatum* Roth.). Its normal life history, external appearance, habitat, and size at maturity are quite familiar to students of algae. Although little is known of the cytology of the zoospores and gametes, and the germination of the resting spores and polyeders, the general organization, with some details of the vegetative nuclear divisions and methods of forming spores and starch, have been described by VAUCHER, BRAUN, PRINGSHEIM, ARTARI, KLEBS, TIMBERLAKE, and HARPER.

In April 1912, shortly after Professor CHAMBERLAIN'S return from an extensive trip through Australia and South Africa, some soil was sent to him by Miss EDITH STEPHENS of the South African College. The soil was secured on the Valkenberg Vlei, near Cape Town, and was supposed to contain spores of the liverwort *Riella*. Some individuals of *Riella* appeared in the culture, but in addition to these there appeared a new species of *Hydrodictyon*, which we shall call *H. africanum*. The following description is based upon the material from this culture.

Early in May there appeared on the bottom of the tank, just above the surface of the soil, a number of green spherical bodies of barely recognizable size, which had the general aspect of *Botrydium*. As growth progressed, the spherical bodies, instead of being groups of solitary cells, were seen to be connected into nets. The nets are made up of 60 or more globular cells which form irregular meshes, arranged in hexagons, heptagons, or octagons, or sometimes simply in broken chains. The nets grow rapidly. Each cell does not grow into an ellipsoidal cylinder as in *H. reticulatum*, but remains spherical or oblong. The cells have remarkable

turgidity, so that when the net is supported at one end, the entire plant is kept straight and can be held up in any position without bending or drooping. When the plants grow larger, the turgidity of the cells remains the same, but the connection between cells is by only a small portion of the surface and consequently it is impossible to move the plant without breaking the cells apart. As the plant grows, the connection becomes less and less secure, so

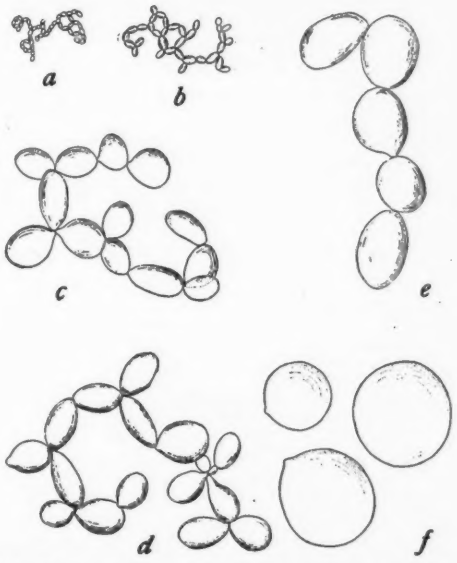


FIG. 1.—*Hydrodictyon africanum*, showing successive stages of development: *a*, May 2, 1912; *b*, May 12; *c*, May 20; *d*, June 12; *e*, June 20; *f*, October 12.—Sketches from living material, natural size.

that the cells fall apart at the slightest touch or even by a movement of water caused by small crustaceans, until finally the nets are broken apart into solitary cells, or coenobia. During this development, the coenobium has reached an enormous size, the diameter often being more than 1.5 cm. Sketches from living material in successive stages from late April to the middle of June are shown in fig. 1.

The dissociated cells remained up to the end of June, and then apparently began to disorganize. Finally they disappeared, and either the entire stock has died or has sunk to the bottom and become buried in the soil in the resting spore or polyeder stage. That the plants should have broken up into solitary cells and that they should have reached such an enormous size might have been thought to be due to the change of environmental conditions, like change in habitat, the gradual change in the density of the water in the tank, or changes in temperature and food. However, another supply of the material, collected in October in the original locality by Miss STEPHENS, showed that the form behaves similarly in nature. This material consists of the various stages as they appeared in the culture, from the young nets of small cells, through broken chains made up of a smaller number of larger cells, to the solitary coenobia. Fig. 1, *f*, shows the last stage, in which the coenobium is slightly larger than those obtained in our own cultures.

It is now clear that the form in nature passes through the same course of development as in our cultures in the laboratory, that is, there is first a net, the cells of which break apart by their own peculiar turgidity and looseness of connection, until finally, the cells which were the sides of the meshes of the net become solitary and live for several months as independent forms. This habit shows most clearly the colonial organization of *Hydrodictyon*.

The soil before starting the culture in the laboratory was not examined for the possible presence of *Hydrodictyon*, but there could be no reason to suspect the previous existence of the plant in the net form in the dried condition, and therefore it must have been in the resting spore condition, characteristic of green algae, or in the polyeder condition, if this form follows the life cycle of *H. reticulatum*, as described by PRINGSHEIM. In any event, we first recognized a rather irregular net coming out of the soil in the tank, which recalls, according to PRINGSHEIM, the product of the germination of a polyeder, though in his description the product consisted of 200–300 cells, while in *H. africanum* there are at most less than 70 cells. The formation of new nets inside the mother cell, which is familiar in *H. reticulatum*, was not observed in this form. The formation of gametes was not observed in the living condition, but

was found in fixed material. Consequently, the final product of the coenobium may be gametes, which escape from the cell and after fusion form resting spores. These directly or with the interpolation of a polyeder stage may repeat the cycle.

Not only does this form differ from *H. reticulatum* in size and habit, but there are points of fundamental difference in the structure of the cell, the most remarkable of which are the presence of numerous definite plastids and the formation of starch, not by the fragmentation from the pyrenoid, but in the plastids. These characters which differ from *H. reticulatum* seem to us to be a sufficient basis for a new species, which may very properly be called *Hydrodictyon africanum*.

The general cell structure, nuclear division, and starch formation deserve a brief account. The protoplast of the coenobium is surrounded by a thick wall and occurs as a thin parietal layer, a large vacuole occupying the center. The cell wall consists of three different layers. The protoplasm may be conveniently described as consisting of three parts: *Hautschicht*, the outermost part, directly in contact with the cell wall; plasma membrane, the innermost part which lines the central vacuole; and between these two the main cytoplasmic body, which contains numerous nuclei, plastids, pyrenoids, starch grains, and small vacuoles (fig. 2).

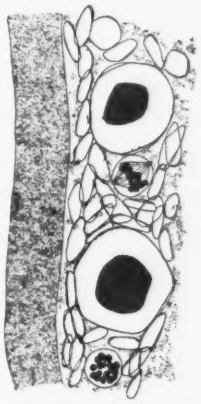


FIG. 2.—Part of a section of a single coenobium: fixed May 20, 1912.—×1500.

The nucleus varies greatly in size at different stages of the division (fig. 3). In the resting stage it is very small, about as large as the shorter diameter of the plastid. It then gradually increases in size. There is a scanty chromatin network and a single nucleolus. When the nucleus has reached its full size, the nuclear network becomes impregnated with a large amount of chromatin. Knots appear in the network and eventually develop into 18 chromosomes. The nuclear membrane is always present until just after metaphase. A centrosome is recognizable from prophase to late anaphase. After telophase, new daughter nuclei

are formed, which grow and divide. No case of amitosis was observed. The mitoses in the cell do not take place simultaneously, so that every stage in the division is shown even in a single section of the cell.

The presence of definite chromatophores or plastids has been a matter of discussion among various workers on *H. reticulatum*, but in this new form numerous plastids lie in contact with one another in the middle part of the cytoplasm. The plastid in its earlier stages has an irregular platelike or spindle-like form, and it is denser in the outer region than in the center. A most interesting and important feature in the new form is that the plastids

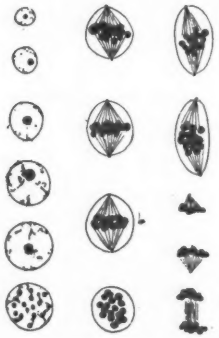


FIG. 3.—Mitotic figures of various stages.—×1500.

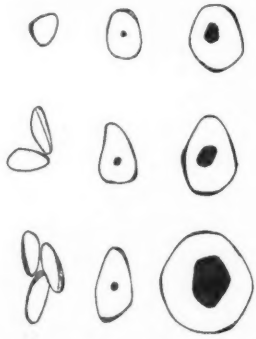


FIG. 4.—Stages showing the formation of pyrenoids from plastids.—×1500.

have two functions, one to produce characteristic pyrenoids and the other to form reserve starch grains.

The formation of pyrenoids from the plastids is as follows. The plastid at first is more dense in the outer part than in the center; and then it increases in size. A deeply staining portion differentiated from the plastid first appears in the center of the body as a small dot, during the growth of the plastid. As the general outline of the plastid grows, the dot also grows, and finally the body of the plastid reaches its full size and assumes a somewhat spherical or slightly angular form; the dot inside also enlarges and assumes a spherical or slightly angular shape. Thus there is established the

so-called pyrenoid, spherical in form and consisting of a denser central portion surrounded by the body of the plastid (fig. 4).

The formation of starch grains by the direct fragmentation of the pyrenoid as described by TIMBERLAKE does not occur in this new form. The method of starch formation is as follows. In a part of the body of the plastid near its margin a starch grain is formed either by secretion, as MEYER believes, or in some other way. The starch grain grows and finally reaches a size equal to that of the pyrenoid. The starch thus formed is more abundant toward the plasma membrane (fig. 5).

FIG. 5.—Stages showing the formation of starch grains by plastids.—×1500.

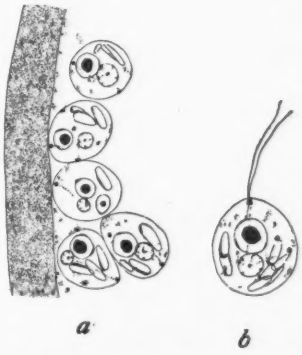


FIG. 6.—Gametes: *a*, part of a section showing the gametes lying near the cell wall, ×1200; *b*, a single gamete, ×1500.

The gamete formation was not observed in living cells, but in fixed material many cases of cells were observed in which a majority of the spores had escaped, still leaving a number of spores within. Whether the spores are zoospores or gametes was not ascertained, but judging from the condition in *H. reticulatum* they should be gametes.

Hydrodictyon africanum Yamonouchi, sp. nov.—Young net of about 60 coenobia; when old, coenobia becoming solitary by breaking apart on account of their great turgidity and loose connections; coenobia deep green, but yellow with age, spherical or oblong, and finally attaining an enormous size, as large as 1.5 cm.; the coenobia live a long time in the solitary condition.

TYPE LOCALITY.—Valkenberg Vlei, near Cape Town, South Africa.

UNIVERSITY OF CHICAGO

REVEGETATION OF A DENUDED AREA

H. S. CONARD

(WITH TWO FIGURES)

One-half mile west of Cold Spring Harbor station on the Long Island Railroad, extensive changes in the roadbed are in progress. In straightening, widening, and changing the grade of the road, the hillside has been cut away, and the materials so obtained have been dumped directly downhill from the cut to make a wide level shelf for the tracks. Where the new level crosses the old grade of the hillside, the soil was practically undisturbed and a curved line of vegetation has grown up from the old roots. On the side of this line toward the hill the earth is newly exposed. It has been buried since the glaciers left it. On the other side of the line, the ground consists of the material dug away from the adjacent hill by steam shovels and dumped at once or after a short haul in cars. The digging was done in March and April 1911. The material moved is coarse sand and fine gravel of the morainic hills of the north side of Long Island. The hillside faces south, and was clothed with a vegetation typical of such a dry, sunny situation in this region.

On the apparently denuded area, the prospective roadbed, many plants are already (July 1911) well developed. A study of the nature and origin of these has proven of interest and is here presented. Sixty species of angiosperms and one fern make up the present flora of the newly made shelf; 53 of these are now to be found growing on the hillside above the cut. Of the plants found both above and below, 39 are long-lived perennials. All of these except *Smilacina racemosa*[1] and *Desmodium canescens* were growing in the made ground from pieces of root, rhizome, or "crown" of old plants carried down from the hillside in the digging. The fragments had been tumbled in promiscuously with the earth, and those near enough the surface had sprouted. Thus we have a large experiment in the roughest kind of transplanting of 37 species

[1] The nomenclature of the new GRAY'S *Manual* has been followed.

during their resting period. The *Smilacina* and *Desmodium* mentioned above grew in the band of vegetation where the old hillside grade intersects the new level. They had not been transplanted, but were covered with about three inches of fresh sand.

Whether the transplants were roots or rhizomes is of but slight importance. So far as we could determine by surface inspection, root propagation is shown by the following:

Myrica Gale, M. asplenifolia (root 6 in. by ½ in.), Sassafras variifolium (6 in. by ¼ in.), Rubus villosus (3 in. by ⅛ in.), Robinia Pseudo-Acacia (4–6 in. by ⅛ in.), Lespedeza fruticosa (?), L. repens, Euphorbia Ipecacuanhae, Rhus glabra (6–8 in. by ½ in.), R. copallina (6 in. by $\frac{3}{16}$ in.), Vaccinium pennsylvanicum (4 in. by ⅛ in.), Asclepias amplexicaulis (3 in. by ½ in.).

Pieces of rhizome give rise to new plants in the following:

Pteris aquilina, Smilax glauca, S. rotundifolia, Aralia nudicaulis (14 in. by ½ in.), Lespedeza virginica (?).

The entire plant or the crown with more or less of root had been moved down bodily in the following:

Andropogon scoparius, Panicum sp., Cyperus filiculmis, Stenophyllus capillaris, Carya alba (stump), Quercus marylandica (stump), Q. alba (stump), Rumex acetosella, Prunus serotina (stump), Baptisia tinctoria, Desmodium nudiflorum, D. rotundifolium, Stylosanthes biflora, Oxalis corniculata, Helianthemum canadense, Viola pedata, Thaspium aureum (?), Plantago major, Eupatorium hyssopifolium, Solidago altissima, S. odora (?), S. tenuifolia, Aster (2 spp. not identified), A. linariifolius, Sericocarpus asteroides, Achillea millefolium, Taraxacum officinale.

Seedlings of the following plants were found in the congenial sand of the new exposure, though no seedlings of *Myrica*, *Castanea*, *Baptisia*, or *Tephrosia* were seen on the hillside. The other species named, whose seedlings were found in both habitats, are nearly all annuals.

Myrica asplenifolia, Castanea dentata, Phytolocca decandra, Mollugo verticillata, Portulacca oleracea, Baptisia tinctoria, Tephrosia virginiana, Trichostema dichotoma, Linaria canadensis, and Ambrosia artemisiaefolia.

The following plants of the new ground were not found at all on the hillside:

Avena sativa, Polygonum hydropiper (?), P. convolvulus, Acalypha virginica, Oenothera biennis, Xanthium canadense (?).

These are such common weeds everywhere that their appearance causes no surprise. Nevertheless it would be interesting to know how they came in. *Avena*, of course, and perhaps others were brought by horses.

Turning to the hillside, we find 25 species[2] which are not yet represented on the new ground below. A few of these deserve notice. For example, a part of the hill is literally covered with

FIG. 1.—A wide level shelf for the track

Gerardia pedicularia, both rosettes and flowering plants. Why did none of these survive transplanting? Perhaps their parasitic habits are partly responsible. If so, the plant must be an obligate parasite, even if only hemiparasitic. *Deschampsia flexuosa* is much more plentiful on the hillside than *Andropogon*, but none of it

[2] The plants found on the hillside but not below are Deschampsia flexuosa, Carex (2 spp.), Corylus americana, Quercus stellata, Amelanchier canadensis, Lupinus perennis, Linum virginianum, Acer rubrum, Psedera quinquefolia, Hypericum gentianoides, Lechea villosa, L. intermedia, Cornus sp., Chimaphila maculata, Gaylussacia baccata, Verbascum Thapsus, Gerardia pedicularia, G. flava, Chrysopsis mariana, Solidago bicolor, Antennaria neglecta, Erechtites hieracifolia, Hieracium venosum, and H. scabrum.

appears below. The new exposure is very sunny, and therefore unfavorable to *Deschampsia*. Perhaps also its root system may not be disturbed without serious injury. Two species of *Lechea* and one of *Hieracium* (*H. venosum*) are the next most plentiful hillside plants which did not survive transplanting. We have no explanation for this. Large clumps of *Lupinus perennis* and *Tephrosia virginiana* occur at one part of the hill. It seems strange

FIG. 2.—On the apparently denuded area many plants are already well developed

that no transplanted specimens were found. The remaining species of the hill were not numerous enough to give any large chance of their finding a possibility of survival on the new ground.

The meaning of this record is in several respects very clear. (1) An area denuded in winter or early spring receives few if any disseminules by any agency save that of man and domestic animals. Plants are not traveling at that season. (2) An apparently denuded area may contain viable fragments of a rather large flora. (3) If the disturbance occurs during the resting season of vegetation, new plants will arise from many fragments which would perish at any other season. For the resting plant contains nourishment to enable

it to start new growth, and most perennials put out a whole new system of absorptive roots as well as a whole new foliage each year. The extent of the new root system is greater than many people suppose. (4) As a corollary to this it follows that most plants can be successfully transplanted, even by very rough methods, during the resting period. This is why I can get three good grape vines by mail in a package but little bigger than a lead pencil, and all of them grow vigorously. It is, indeed, the basis of the whole nursery business. (5) Propagation from bits of resting roots and rhizomes is possible in many plants where this method is not usually practiced. But the practice has become much more common commercially in the last ten years, owing to the keen observation of the best gardeners. It must be stated that in many cases of the transplants noted in this account, the new rootage seemed more meager than the production of shoots. Whether all of the sixty-one species will survive, or, in the terminology of CLEMENTS, whether their rather violent migration will be followed by ecesis, remains to be seen.

COLD SPRING HARBOR, L.I.

CURRENT LITERATURE

NOTES FOR STUDENTS

Metabolism of fungi.—The problem of the necessity of calcium for fungi has been attacked in different ways by HORI and by Mlle. ROBERT. HORI[1] relied on removing the calcium from his solutions by precipitating it by means of an oxalate. To a solution of "ame" (rice treated with malt extract) in bouillon, he added potassium sulphate and potassium oxalate. In the solution thus obtained *Aspergillus niger*, *A. flavus*, and *Penicillium glaucum* developed well, while *Cephalothecium roseum*, *Rhizopus nigricans*, *Rammularia Citri*, *Botrytis tenella*, *Sclerotinia Libertiana*, and a species of *Entomophthora* developed poorly or not at all. All the fungi developed well in the same solution to which potassium sulphate but no oxalate had been added. From the fact that a number of the fungi did not develop in a solution containing 0.5 per cent of potassium oxalate, the author concludes that these probably require calcium for their development. The conclusion is scarcely justified, since it is not at all probable that calcium is completely removed by potassium oxalate from solutions containing organic substances. The same criticism applies to the experiments of WEIR, which have already been reviewed in this journal.[2]

The problem has been attacked in a more critical manner by Mlle. ROBERT,[3] who worked with *Aspergillus niger*. She showed that the results of the earlier investigators (RAULIN, MOLISCH, LOEW), who came to the general conclusion that calcium was not necessary for the life of most fungi, were due to the fact that they relied on the so-called "pure salts" of commerce. Mlle. ROBERT finds that these "pure salts" always contain calcium. It is thus evident that the conclusion generally reached by those investigators, that calcium is not necessary for the life of fungi, was reached on insufficient grounds. Mlle. ROBERT purified the salts she used until no traces of calcium could be detected in them. In culture solutions made from such purified materials *Aspergillus niger* grows equally well whether calcium is added or not. From dilute solutions containing up to 2.5 mg. per 250 cc. of solution, the calcium is removed almost quantitatively by the fungus and can be recovered in the ash. From stronger solutions containing 10–100 mg. per 250 cc. about 80 per cent of the calcium is removed. When much calcium is absorbed, both the yield and

[1] HORI, S., Haben die höheren Pilze Kalk nötig? Flora **101**:447, 448. 1910.

[2] BOT. GAZ. **53**:88. 1912.

[3] ROBERT, MLLE., Influence du calcium sur le développement et la composition minérale de l'*Aspergillus niger*. Compt. Rend. **153**:1175–1177. 1911.

the ash of the fungus are increased, but the increase corresponds to the amount of calcium absorbed. The increase of the ash corresponds to the amount of calcium absorbed calculated as calcium carbonate. It appears from this paper that calcium is of no importance for the development of *Aspergillus niger*, but that when present in the culture medium, it is absorbed and increases the yield and ash only by the amount absorbed.

In another paper[4] Mlle. ROBERT concludes that the calcium absorbed from solutions by *Aspergillus niger* is quantitatively fixed in the form of calcium oxalate. This conclusion is based on analyses of mycelia from a large number of cultures. Although it was necessary to determine the calcium and the oxalic acid in different cultures, the determinations showed that the oxalic acid present in the mycelium corresponded to the quantity calculated on the assumption that all the calcium fixed was present in the form of calcium oxalate. Owing to the fact that in the cultures without calcium the oxalic acid formed diffuses into the medium, mycelia from such cultures always contain less oxalic acid than those with calcium.

SAUTON,[5] studying the effect of iron on spore-formation of *Aspergillus niger* grown on RAULIN'S solution free from iron, finds that in the absence of iron no spores are formed by this fungus. This fact, while not mentioned specifically by RAULIN, seems nevertheless not to have escaped his notice completely, for he states that in the absence of iron spores become fewer and fewer in proportion to the number of crops of fungus grown on the same solution. When iron is added to cultures free from iron, the yield increases and spores are produced. Cultures with 0.1 mg. of iron per 100 cc. of liquid and those with 1.0 mg. per 100 cc. gave practically the same yield, but spore-formation was almost suppressed in the 0.1 mg. cultures, while those with 1.0 mg. per 100 cc. were black with spores. The cultures without iron made feeble growth and produced no spores. Since there was no difference in growth but a great difference in spore-production between cultures containing 0.1 mg. of iron per 100 cc. of liquid and those containing 1.0 mg. per 100 cc., the author concludes that iron has a specific influence on spore-formation. The possibility that toxic substances are produced in the absence of iron had already been suggested by RAULIN, who noted that in cultures without iron a substance is formed which he regarded as sulphocyanic acid, and FERNBACH had shown that in the presence of ammonium sulphocyanate *Aspergillus niger* grows naturally but does not form spores. SAUTON doubts the formation of sulphocyanic acid, since the liquid from cultures containing 0.1 mg. of iron per 100 cc. (in which spore-formation is almost inhibited) does not give the red color reaction with ferric salts. In cultures without iron, however, a faint red color reaction

[4] ROBERT, MLLE., Mode de fixation du calcium par l'*Aspergillus niger*. Compt. Rend. **154**: 1308–1310. 1912.

[5] SAUTON, B., Influence du fer sur la formation des spores de l'*Aspergillus niger*. Compt. Rend. **151**: 241–243. 1910.

indicating colorometrically a concentration of 0.005 per cent of sulphocyanic acid could be obtained, but the equivalent of that concentration of ammonium sulphocyanate is without effect on the fungus. That other poisonous substances are formed is doubted by the author, because if to a solution free from iron, on which *Aspergillus* has grown for three days without forming spores, iron is added the culture becomes covered with spores in 24 hours. The suppression of spore-formation is therefore due to the lack of iron and not to a toxic substance. Furthermore, since ferric sulphocyanate also inhibits spore-formation, the favorable effect of iron cannot be due to a possible neutralization of sulphocyanic acid by iron. The author notes a similarity in the behavior of cultures without iron and those suffering from lack of oxygen, and suggests that iron is possibly instrumental in bringing about oxygen fixation.

RAULIN'S observation, confirmed by SAUTON, of the occurrence in cultures of *Aspergillus* of a substance giving a red color reaction with ferric salts and therefore regarded as sulphocyanic acid, is of interest in view of the fact that GOSIO in Italy and ALSBERG and BLACK in this country find in cultures of other molds phenol-like substances giving red color reactions with ferric salts.

A later paper by SAUTON[6] consists essentially of a republication of the foregoing paper with some additional observations, although in the meantime the author working with JAVILLIER had published results (reviewed below) leading to an entirely different conclusion from that reached in these two papers. It appears from SAUTON'S second paper that the need of iron is not general among fungi, for while *Aspergillus niger*, *A. fumigatus*, *Penicillium glaucum*, and *P. candidum* make only feeble growth on RAULIN'S solution free from iron, *Mucor Mucedo*, *Rhizopus nigricans*, and *Racodium coellare* thrive well without iron, or at least with only such minute traces of it that it is impossible to detect them. Since the publication of SAUTON'S first paper, BERTRAND and JAVILLIER have called attention to the effect of manganese on the growth of *Aspergillus niger*, without however giving attention to the influence of that element on spore-production. SAUTON finds that the substitution of manganese for iron also stimulates spore-production. He has not been able, however, to obtain sulphate of manganese, which he employed, entirely free from iron, and although the traces of iron thus added were extremely minute, he does not draw any conclusion as to the possibility of substituting one of these elements for the other. Further evidence that the inhibition of spore-production is not due to the formation of sulphocyanic acid was obtained from an experiment in which both sulphur and iron were absent. Although the formation of sulphocyanic acid was not possible under these conditions, spore-production was nevertheless inhibited. On the addition of sulphate of iron spores were formed, showing that it is not sulphocyanic acid which inhibits spore-formation.

[6] SAUTON, B., Influence du fer sur la culture de quelques moisissures. Ann. Inst. Pasteur **25**:922–928. 1911.

Conclusions very different from the foregoing regarding the special rôle of iron in spore-formation are reached by JAVILLIER and SAUTON[7] in the paper mentioned above. According to this paper iron does not possess a special rôle in the formation of spores, but in the absence of iron, spore-formation is inhibited by the zinc in RAULIN's solution. If both zinc and iron are excluded, spores are readily formed, just as they are when both of these elements are present. If zinc alone is present, spore-formation is inhibited.

The authors suppose that the zinc, which was observed by RAULIN to have a favorable effect in the culture solution proposed by him, exerts toxic effects when the mycelium is poorly nourished through the lack of iron or from some other cause. In the ash of mycelia grown on solutions without iron, no iron was found, although the reactions employed were capable of indicating the presence of 1/1000 of a milligram of the element; hence the authors conclude that if iron is at all essential for spore-formation, the quantity required is so small that it cannot be detected in the ash of the mycelium. It is also stated that the substance giving the red color with ferric salts and supposed by RAULIN to be sulphocyanic acid is not formed when both iron and zinc are absent.

A search for an explanation of the favorable effect, noted by RAULIN and others, of zinc on the growth of *Aspergillus* has led JAVILLIER[8] to investigate the action of that metal on the secretions of invertase by *Aspergillus niger*. The results are suggestive as showing the influence of certain substances on the diffusion of other substances through the protoplasmic membrane. He finds that in cultures free from zinc the liquid does not invert sugar, while culture solutions containing zinc invert sugar readily after *Aspergillus niger* has been grown on them. This difference, however, does not indicate that no invertase is formed in the absence of zinc, for sugar was consumed in both cultures. In cultures free from zinc the enzyme does not diffuse into the liquid.

Several notes have been published by BERTRAND and by BERTRAND and JAVILLIER on the influence of manganese on *Aspergillus niger* and on the relations of this element to zinc and iron when present in the culture medium. Manganese[9] in dilute solutions is found to have a favorable action on the growth of this mold. In solutions containing manganese in concentrations ranging from 1 part in 1,000,000 to 1 part in 100, there was a gradual increase

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[7] JAVILLIER, M., et SAUTON, B., Le fer est-il indispensable à la formation des conidies de l'*Aspergillus niger?* Compt. Rend. **153**:1177–1180. 1911; also Compt. Rend. Soc. Biol. **71**:589, 590. 1911.

[8] JAVILLIER, M., Influence de la suppression du zinc du milieu de culture de l'*Aspergillus niger* sur la sécrétion de sucrase par cette Mucédinée. Compt. Rend. **154**:383–386. 1912.

[9] BERTRAND, G., et JAVILLIER, M., Influence du manganèse sur le développement de l'*Aspergillus niger*. Compt. Rend. **152**:225–228. 1911; also Bull. Sci. Pharmacologique **18**:65–73. 1911; also Bull. Soc. Chim. France. pp. 212–220. 1912.

of yield with increasing concentration of the metal. An increasing quantity of the metal was found in the ash, although even in dilute solutions the element was not removed quantitatively, like calcium or zinc. A concentration of 1 part in 50 was deleterious.

Unexpected results[10] showing the sensitivity of plants to extraordinarily minute traces of substances were obtained with manganese in extreme dilutions. After every available means had been used for removing manganese from the ingredients of the culture solutions, it was found that the addition of 1 mg. of manganese in 1,000,000 liters produced a marked increase in yield, while in some cases even the effect of 1 mg. in 10,000,000 liters was noticeable. The effect of manganese in such extreme dilutions is attributed to action of a catalytic nature. The necessity of taking into consideration in physiological experiments the possibility of effects being produced by such minute traces of substances which may be present as impurities in the materials used is pointed out.

The simultaneous addition[11] of zinc and manganese in concentrations at which these metals individually increase the yield of fungus produces a greater yield than the addition of either metal alone. The favorable concentrations were: zinc, 1 part in 100,000 to 1 part in 25,000,000; and manganese, 1 part in 500 to 1 part in 25,000.

To determine if either of these two metals exerted an influence on the absorption of the other, the quantity of manganese absorbed in the presence of zinc was compared[12] with that absorbed from solutions without zinc. The results show that in general the percentage of manganese in the dry weight of the fungus is greater in the presence of zinc. The proportion varies somewhat according to the concentrations of manganese and zinc. The effect of the zinc is more marked in dilute solutions and disappears in more concentrated solutions.

To manganese is attributed a special rôle in spore-formation formerly ascribed by RAULIN and by SAUTON to iron. The effect noted by these investigators BERTRAND[13] believes to be due to the introduction of minute traces of manganese from which it is difficult to free some of the other salts used in RAULIN's solution. He finds that when *Aspergillus* is grown in a solution free from manganese, but containing both zinc and iron (1 part in 100,000) no

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[10] BERTRAND, G., Extraordinaire sensibilité de l'*Aspergillus niger* vis-à-vis du manganèse. Compt. Rend. **154**:616–618. 1912.

[11] BERTRAND, G., et JAVILLIER, M., Influence combinée du zinc et du manganèse sur le développement de l'*Aspergillus niger*. Compt. Rend. **152**:900–902. 1911; also Bull. Sci. Pharmacologique **18**:321–327. 1911.

[12] ———, Influence du zinc et du manganèse sur la composition minerale de l'*Aspergillus niger*. Compt. Rend. **152**:1337–1340. 1911.

[13] BERTRAND G., Sur le rôle capitol du manganèse dans la formation des conidies de l'*Aspergillus niger*. Compt. Rend. **154**:381–383. 1912.

spores are produced. If a trace of manganese is added, the surface becomes black with conidia.

A later paper by BERTRAND and JAVILLIER[14] consists of recapitulation of the data in the foregoing papers by them, together with a general discussion of the results obtained.

The availability of various nitrogenous compounds as sources of nitrogen for fungi has been investigated by BRENNER, by RITTER, and by KOSSOWIG. BRENNER[15] in a brief paper gives the general results of an investigation designed to determine the relative value of various nitrogenous compounds for the nutrition of *Aspergillus niger*. The compounds were given in a concentration equivalent in nitrogen to a 0.5 per cent ammonium chloride solution. The nutritive value of the substances was determined by ascertaining the time required for the cultures to attain a maximum weight on a given substance. Both the time required for reaching a maximum development and the weight of fungous substance produced were taken into consideration. By analysis of the fungus crops and the residual culture medium, the qualitative and quantitative interchange of nitrogen between the fungus and the medium was determined. The results showed that a large number of compounds are not suitable sources of nitrogen. Of this category are free ammonia, sodium nitrite, ammonium valerianate, and potassium cyanide, all of which are poisonous, and tetramethylammonium chloride, nitroguanidin, nitromethane, isoamylacetate, pyridin chloride, and piperidine chloride, which are not assimilable. The order of nutrient value of the other compounds tried is somewhat as follows: first, ammonium lactate, ammonium tartrate, asparagin, ammonium succinate, and ammonium oxalate; second, the ammonium salts of sulphuric, hydrochloric, nitric, and phosphoric acids, and carbamid; third, ammonium acetate, ammonium formate, nitrosodimethylamin chloride, sodium nitrate, pyridin nitrate, normal and isobutylamin chloride, guanidin nitrate, and guanidin chloride. Of less nutritive value are isoamylamin chloride, hydroxylamin sulphate, benzylamin sulphate, dicyandiamid, and perhaps acetonitril.

A study of the composition of the fungus and the changes in the medium showed that after a period of growth of about 4 days, processes of degeneration began in parts of the fungus. These were accompanied by the secretion of nitrogen as ammonia or as organic nitrogenous compounds. As a rule, regardless of the nature of the compounds, about one-half of the nitrogen present in a solution containing the nitrogen equivalent of a 0.5 per cent ammonium chlorid solution was taken up by the first crop of fungus grown. Subsequent crops having less nitrogen at their disposal contained a lower percentage of

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[14] BERTRAND, G., et JAVILLIER, M., Action du manganèse sur le développement de l'*Aspergillus niger*. Ann. Inst. Past. **26**: 241–249. 1912.

[15] BRENNER, W., Untersuchungen über die Stickstoffernährung des *Aspergillus niger* und deren Verwertung. Ber. Deutsch. Bot. Gesells. **29**: 479–483. 1911.

nitrogen than the first crops on the same solution. No general conclusions were deducible from a quantitative study of the residual culture fluid.

RITTER[16] in confirmation of results published in a former paper emphasizes the fact that *Aspergillus glaucus*, *Cladosporium herbarum*, and *Mucor racemosus*, known as "nitrate fungi" on account of their supposed preference for nitrogen from the nitrate ion, thrive equally well or better on ammonium salts. The slight alkalinity arising in cultures with potassium nitrate is, according to him, not the cause of the depression of growth in such cultures. The assimilation of nitrogen from nitrates takes place by means of a reduction of the nitrates to nitrites, as in bacteria and the higher plants. Since nitrites are not stable in acid solutions, it is necessary to keep the cultures neutral or alkaline to show the formation of nitrites. In such cultures nitrites resulting from the reduction of nitrates were shown to occur.

KOSSOWICZ[17] examined a number of fungi with reference to their ability to obtain nitrogen from calcium nitrid supplied in a nutrient solution containing per liter 2.5 gms. dipotassium hydrogen phosphate, 0.5 gms. magnesium sulphate, 25 gms. cane sugar, and 5 gms. tartaric acid. The calcium nitrid was added after sterilization. The fungi used were *Botrytis bassiana*, *Penicillium crustaceum*, *P. brevicaule*, *Mucor Boidin*, *Cladosporium herbarum*, *Phytophthora infestans*, *Aspergillus glaucus*, *A. niger*, *Isaria farinosa*, and a species of *Fusisporium*. Of these only *Phytophthora infestans*, *Botrytis bassiana*, and *Mucor Boidin* showed any growth after three months. *Phytophthora infestans* caused the production of ammonia in the culture medium, but in the cultures of the other two fungi ammonia could not be detected with Nessler's reagent. The poisonous effect of calcium nitrid was shown by the feeble growth of the foregoing fungi on solutions containing calcium nitrid and ammonium chloride compared with their growth on solutions containing ammonium chloride alone as a source of nitrogen.

The availability of different phosphorus compounds as sources of phosphorus for *Aspergillus niger* has been studied by DOX.[18] Of the inorganic compounds he finds that orthophosphate, pyrophosphate, and metaphosphate serve well as sources of phosphorus, while hypophosphite and phosphite containing trivalent phosphorus, while not toxic, do not supply phosphorus in an available form. Several organic substances containing phosphorus were found to be excellent sources of phosphorus for the mold. The substances tested were phytin, sodium glycerinophosphate, sodium nucleinate, lecithin, casein, and ovovitellin. The author suggests that in all these cases phosphoric

[16] RITTER, G. E., Ammoniak und Nitrate als Stickstoffquelle für Schimmelpilze. Ber. Deutsch. Bot. Gesells. **29**:570–577. 1911.

[17] KOSSOWICZ, A., Über das Verhalten einiger Schimmelpilze zu Kalkstickstoff. Zeitschr. Gärungsphysiologie **1**:124, 125. 1912.

[18] DOX, A. W., The phosphorus assimilation of *Aspergillus niger*. Journ. Biol. Chem. **10**:77–80. 1911.

acid is first split off from the organic compound by means of enzymes. This suggestion is strengthened by the facts that IVANOFF has prepared an enzyme from this mold which decomposes nucleic acid with the liberation of phosphoric acid, and the author himself has shown the presence in another mold of an enyzme capable of hydrolyzing casein.—H. HASSELBRING.

Current taxonomic literature.—O. AMES (Phil. Journ. Sci. Bot. **7**:1–27. 1912) in continuation of his studies in the Orchidaceae has published 27 new species of orchids from the Philippine Islands.—O. BECCARI (Pomono Coll. Journ. Ec. Bot. **2**:253–276. 1912) under the title "Palms indigenous to Cuba I" recognizes 14 genera, 3 of which are treated in detail in the present paper. One new species is added to the genus *Oreodoxa*, namely *O. princeps*.—C. H. BISSELL and M. L. FERNALD (Rhodora **14**:91, 92. 1912) record a new variety of *Lespedeza* (*L. capitata* var. *stenophylla*) from Illinois and Connecticut. G. BITTER (Rep. Sp. Nov. **10**:489–501. 1912) places on record supplementary data to his recent monograph of the genus *Acaena* and includes descriptions of new varieties from Central and South America. The same author (*ibid.* 529–565) under the title "Solana nova vel minus cognita I" has published 36 new species of *Solanum* also from Central and South America.—S. F. BLAKE (Rhodora **14**:102–106. *pl. 94.* 1912) characterizes several new forms of *Peltandra virginica*.—E. BRAINERD (Bull. Torr. Bot. Club **39**:85–97. *pls. 5–7.* 1912) presents an interesting article on "Violet hybrids between species of the *palmata* group," recording several new hybrids in the genus.—A. BRAND (Univ. Calif. Pub. Bot. **4**:209–227. 1912) presents a preliminary consideration of the Hydrophyllaceae of the Sierra Nevada region. Several new varieties and forms are described and certain changes in nomenclature are made. The same author (Phil. Journ. Sci. Bot. **7**:29–36. 1912) records the results of further investigations on the Symplocaceae of the Philippine Islands, adds 3 new species to *Symplocos*, and gives a revised key to the 26 recognized Philippine species of this genus.—T. S. BRANDEGEE (Univ. Calif. Pub. Bot. **4**:269–281. 1912) under the title "Plantae Mexicanae Purpusianae IV" has published 29 new species and 2 varieties of flowering plants. One new genus (*Oxyrhynchus*) of the Leguminosae is proposed.—H. BRAUNS (Verhandl. K. K. Zoolog.-Bot. Gesell. Wien **61**:139–143. 1911) describes 6 new species of *Nitella*, 2 of which are from Costa Rica.—J. BROADHURST (Bull. Torr. Bot. Club **39**:257–278. *pls. 21, 22.* 1912) under the title "The genus *Struthiopteris* and its representatives in North America" gives a revision of the genus, recognizing 9 species, of which 2 are new to science.—J. BURTT-DAVY and R. POTT-LEENDERTZ (Ann. Transvaal Mus. **3**:119–182. 1912) have issued a check list of the flowering plants and ferns of the Transvaal and Swaziland. Approximately 3240 species are enumerated, representing 920 genera and 157 families.—E. J. BUTLER (Ann. Botany **25**:1023–1035. 1911) describes and illustrates a new genus and species (*Allomyces arbuscula*) of the Leptomitaceae from India.—E. CLAASSEN (Ohio Nat. **12**:543–548. 1912) records about 125 species and varieties of lichens from

northern Ohio.—F. S. COLLINS (Tufts Coll. Studies Sc. Ser. **3**:69–109. *pls. 1, 2.* 1912) in a supplementary paper on "The green algae of North America" records important data on this group of plants and adds several new species, varieties, and forms.—E. B. COPELAND (Philip. Journ. Sci. Bot. 6:359–364. 1911) under the title of "Cyatheae species novae orientales" has published several new to science. The same author (*ibid.* **7**:47–68. 1912) makes important contributions to our knowledge of the fern flora of the Philippines and describes 29 species new to science.—H. N. DIXON (Journ. Bot. **50**:145–156. *pl. 517.* 1912) in continuation of his studies of the mosses of India has published jointly with CARDOT several species new to science and proposes a new genus (*Bryosedgwickia*) of the Entodontaceae.—A. D. E. ELMER (Leafl. Philip. Bot. **4**:1475–1520. 1912) has described 40 new species of flowering plants from the Philippine Islands.—A. W. EVANS (Bull. Torr. Bot. Club **39**:209–225. *pls. 16, 17.* 1912) in continuation of studies in the Hepaticae of Puerto Rico describes and illustrates a new species and variety of *Diplasiolejeunea*.—H. S. FAWCETT (Phytopathology **2**:109–113, *pls. 8, 9.* 1912) has published an account of a new fungus (*Phomopsis citri*) which is said to cause the so-called stem-end rot of citrus fruits.—W. FAWCETT (Journ. Bot. **50**:177–182. *pl. 518.* 1912) has published 9 new species of *Pilea* and a new *Peperomia* from Jamaica.—F. FEDDE (Rep. Sp. Nov. **10**:478–480. 1912) in continuation of his studies on the genus *Corydalis* records 2 new species and a new variety from western and southwestern United States.—M. L. FERNALD and K. M. WIEGAND (Rhodora **14**:115, 116. 1912) record a new variety of *Carex* (*C. scoparia* var. *subturbinata*) from Newfoundland, etc.—H. M. HALL (Univ. Calif. Pub. Bot. **4**:195–208. 1912) under the title "New and noteworthy Californian plants I" records important notes on plants of the region indicated and makes several new combinations as the result of field and herbarium study.—R. HAMET (Notizblatt **5**:277, 278, 1912) has published a new species of *Sedum* (*S. Adolphi*) based on plants cultivated in the Royal Botanical Garden at Dahlem-Steglitz from seeds collected in Mexico by PURPUS.—L. L. HARTER and E. C. FIELD (Phytopathology **2**:121–124. 1912) under the title "*Diaporthe*, the ascogenous form of sweet potato dry rot" describes a new species (*Diaporthe batatatis*).—A. HEIMERL (Oesterr. Bot. Zeitschr. **51**:10, 11. 1911) has published a new species of *Hilleria* (*H. longifolia*) from Peru.—A. A. HELLER, (Muhlenbergia **8**:49–58. 1912) describes a new species of *Castilleja* (*C. lapidicola*) and raises the sectional name *Siphonella* Gray to generic rank, citing *Gilia Nuttallii* Gray as the type of the proposed genus. The same author (*ibid.* 61–71) in continuation of his studies in the genus *Lupinus* describes two new species from Oregon.—F. HEYDRICH (Bib. Bot. Heft 75, pp. 1–21, *pls. 1, 2.* 1911) has proposed the generic name *Crodelia* to which is transferred *Lithophyllum incrustans* Phil. Some 25 forms of this species are indicated under the new combination.—J. HUTCHINSON (Kew Bull. 1912. 223, 224) has published a new *Sapium* (*S. cladogyne*) from British Guiana.—A. KNEUCKER (Allgem. Bot. Zeits. Beilage zu Jahrgang. 1911. pp. 12) has described 3 new species in the Cyperaceae from

the Philippine Islands.—K. KRAUSE (Notizblatt **5**:264, 265. 1912) records 2 new species of *Phoradendron* from Costa Rica. The same author (*ibid.* 266, 267) has published 2 new species of Araceae from the Philippines.—F. D. LAMBERT (Tufts Coll. Studies Sci. Ser. **3**:111–115, *pl. 3.* 1912) describes and illustrates a new genus and species of alga (*Didymosporangium repens*) of the Chaetophoraceae, found on *Antithamnion plumula* at Naples, Italy.—H. LÉVEILLÉ (Bull. Geogr. Bot. **21**:149. 1911) has published a new species of *Epilobium* (*E. Arechavaletae*) from Uruguay.—J. M. MACFARLANE (Contr. Bot. Lab. Univ. Penn. **3**:207–210. *pls. 1, 2.* 1911) has published 2 new species of *Nepenthes* (*N. Merrilliana* and *N. truncata*) from the Philippine Islands.—B. MACKENSEN (Bull. Torr. Bot. Club **39**:289–292. 1912) records 3 new species of *Opuntia* from Texas.—J. H. MAIDEN (Rev. Euclayptus **2**, parts 4–6. pp. 135–216. *pls. 61–72.* 1912) contains descriptions, notes, and illustrations of several different species of *Eucalyptus*.—G. MASSEE (Kew Bull. 1912. 189–191) has described several now species of fungi, including one (*Eutypa gigaspora*) from Trinidad.—E. D. MERRILL (Phil. Journ. Sci. Bot. **7**:71–107. 1912), under the title "Sertulum Bontocense" has described 32 new species of flowering plants from the Island of Luzon, P.I., and proposes a new genus (*Vanoverberghia*) of the Zingiberaceae. The same author (*ibid.* **6**:369–406) presents a synoptical revision of the Philippine species of *Begonia*, recognizing 59 species of which 33 are described as new.—B. NĚMEC (Bull. Int. Acad. Sci. Bohême **16**:67–84. *pls. 1, 2.* 1911) under the title "Zur Kenntnis der niederen Pilze I. Eine neue Chytridiazee" presents a detailed account of a fungus to which he gives the name *Sorolpidium Betae*, nov. gen. et sp.—R. PILGER (Nobizblatt **5**:259–263. 1912) has published 10 new species of *Plantago* from America.—L. RADLKOFER (Phil. Journ. Sci. Bot. **6**:365–367. 1912) proposes a new genus (*Hebonga*) of the Simarubaceae from the Philippine Islands; the genus is represented by two known species.—C. S. SARGENT (Pub. Arnold Arb. No. 4, pp. 145–312. 1912) in cooperation with E. KOEHNE, A. REHDER, C. SCHNEIDER, and E. H. WILSON under the leading title of "Plantae Wilsonianae" has issued the second part of a series of papers dealing with plants collected in western China by Mr. E. H. WILSON in 1907, 1908, and 1910. The paper contains many new species and varieties, particularly in the Saxifragaceae and Rosaceae.—W. A. SETCHELL (Univ. Calif. Pub. Bot. **4**:229–268. *pls. 25–31.* 1912), under the title "Algae novae et minus cognitae I" has published several new species, and proposes the following new genera: *Hapterophycus* of the Ralfsiaceae, *Besa* of the Gigartinaceae, and *Baylesia* of the Dumontiaceae.—J. M. GREENMAN.

The evolution of the chalazogams.—A rather extended paper by NAWASCHIN and FINN[19] describes the morphology of *Juglans nigra* and *J. regia* and discusses the significance of chalazogamy. The paper is in Russian,

[19] NAWASCHIN, S., and FINN, W., Zur Entwickelungsgeschichte der Chalazogamen. *Juglans nigra* und *J. regia*. Mem. Soc. Nat. Kieff **22**:1–85. *pls. 1–4.* 1912.

but there is a summary in German, the principal features of which are as follows: Among the seed plants there is an evident tendency to reduce the male gamete so that the male cytoplasm does not take part in fertilization. In this reduction the binucleate generative cell has played an important part. Its appearance in the gymnosperms (Abietineae, some Taxaceae, Gnetales) is accompanied by a constantly increasing disorganization of the male cytoplasm, which finally leads to the naked sperm nuclei of the higher angiosperms. The species of *Juglans* studied have binucleate generative cells which reach the embryo sac without disorganization, and correspond exactly to the binucleate generative cells of certain gymnosperms. In this feature, therefore, these species occupy an intermediate position between gymnosperms, in which the cytoplasm reaches the egg cell, and the higher angiosperms, in which the male cytoplasm disorganizes in the pollen tube or even in the pollen grain.

The persistence of the male cytoplasm in *Juglans* is thought to be a primitive character retained from their gymnosperm ancestors, and the appearance of this character in chalazogams is said to be significant and is a further proof of the great age of these plants. The tendency in seed plants to reduce the male gametes seems correlated with the appearance of the pollen tube, for the simplification of the male gametes goes hand in hand with the evolution of the pollen tube.

While some of these conclusions seem rather arbitrary, the progressive reduction of the male gametes is a fact which all must recognize. Criticisms are left for those who can read the full paper.—CHARLES J. CHAMBERLAIN.

Winter condition of brown rots.—Conflicting and uncertain statements n the literature regarding the manner in which the fungi producing the brown rots of stone-fruits and pomaceous fruits live through the winter have led EWERT[20] to study the behavior of the conidia of these fungi with regard to their capacity for persisting through the winter. The rarity of the apothecia makes it improbable that these play an important part in maintaining the brown rot fungi.

EWERT finds that the two species of brown rot fungi, *Monilia cinerea* and *Monilia fructigena*, differ radically in their mode of passing the winter, a fact which may account for the discrepancies in the literature, since most of the conflicting statements regarding the persistence of the spores during winter were made before WORONIN had shown that the two species are clearly distinct. EWERT finds that the conidia of *Monilia cinerea*, which occurs primarily on stone-fruits but which can also infect pomaceous fruits, are capable of germinating at any time during the winter. They persist during the winter in the spore-cushions on mummies of cherries, plums, and other stone-fruits, and also on pomaceous fruits if these happen to be infected. Exposure to tempera-

[20] EWERT, E., Verschiedene Überwinterung der Monilien des Kern- und Steinobstes und ihre biologische Bedeutung. Zeitschr. Pflanzenkrank. **22**:65–86. 1912.

tures much lower than those which occur annually at PROSKAV, where the investigations were made, did not injure the germinative capacity of the spores. The mycelium also remains alive and produces new spore-cushions in the spring.

The conidia of *Monilia fructigena*, which occurs chiefly on pomaceous fruits, lose their capacity for germination very early in the winter. The fungus persists solely by means of the mycelium. New spores are produced in the spring, when the mummies covered with the crust-like spore-cushions are soaked and kept in a warm place.

The twig-blight of stone-fruits, which flower early in the season, is caused entirely by *Monilia cinerea*, whose spore-cushions are produced much earlier than those of *M. fructigena*. The spores of *M. fructigena* are not formed at the flowering time of the stone-fruits.—H. HASSELBRING.

Ecology of mosses.—A careful study of the mosses of Isle Royale, Mich., by COOPER[21] proves that there is a well marked succession extending from pioneer conditions to the establishment of the climax forest. From beginnings both upon the rock shore and in the bogs two distinct lines lead to the same climax, characterized by *Calligeron Schreberi*, *Hylocomium proliferum*, and *Hypnum cristacastrensis* as dominant species. The importance of mosses as pioneers upon bare rock surfaces and in peat bogs has long been recognized, but the present study shows that they are of equal importance in the climax forest in promoting the accumulation of humus and in the conservation of soil moisture. This investigation represents a new departure in the field of ecology, and proves not only that the same general laws of succession hold among bryophytes as among seed plants, but that these plants of lower rank may often serve as indicators of the advancement attained by any particular forest association. This latter feature may prove of the greatest value in the study of our northern forests, where the number of tree species is reduced to a minimum.—GEO. D. FULLER.

Calcium-magnesium ratio.—LOEW[22] calls attention to the fact that the results obtained by MEYER and LEMMERMAN in their work on the calcium-magnesium ratio do not agree with those previously worked out by himself. He claims that the results obtained by them were due to the fact that the soi was insufficient in amount for the number of plants grown. The dry weight of their plants was only half the weight of plants grown under ordinary conditions. This dwarfing was due to the arresting of root growth, and no conclusion can be drawn concerning the calcium-magnesium ratios from plants grown under crowded conditions.—JOHN N. MARTIN.

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[21] COOPER, WILLIAM S., The ecological succession of mosses as illustrated upon Isle Royale, Lake Superior. Plant World **15**: 197–213. 1912.

[22] LOEW, OSCAR, Über angebliche Widerlegung der Lehre vom Kalkfaktor. III. Landwirtschaftl. Jahrb. **42**: 181–192. 1912.

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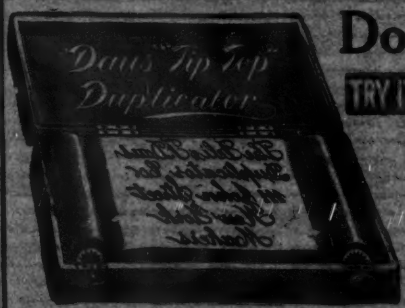

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